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## SPECIES INTERACTIONS AFFECT DISPERSAL: A META-ANALYSIS

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## ABSTRACT

Context-dependent dispersal allows organisms to seek and settle in habitats improving their fitness. Despite the importance of species interactions in determining fitness, a quantitative synthesis of how they affect dispersal is lacking. We present a meta-analysis asking (1) whether the interaction experienced and/or perceived by a focal species (detrimental interaction with predators, competitors, parasites, or beneficial interaction with resources, hosts, mutualists) affects its dispersal, (2) how the species' ecological and biological background affects the direction and strength of this interaction-dependent dispersal. After a systematic search focusing on actively dispersing species, we extracted 397 effect sizes from 118 empirical studies encompassing 221 species pairs; arthropods were best represented, followed by vertebrates, protists and others. Detrimental species interactions increased the focal species' dispersal (adjusted effect: 0.33 [0.06,0.60]), while beneficial interactions decreased it (-0.55 [-0.92,-0.17]). The effect depended on the dispersal phase, with detrimental interactors having opposite impacts on emigration and transience. Interaction-dependent dispersal was negatively related to species' interaction strength, and depended on the global community composition, with cues of presence having stronger effects than the presence of the interactor, and the ecological complexity of the community. Our work demonstrates the importance of interspecific interactions on dispersal plasticity with consequences for metacommunity dynamics.

## INTRODUCTION

The dynamics of local and regional communities result from the distribution and abundance of interacting species [1]. At a local scale, the strength and direction of these interactions affect coexistence and community dynamics. At a regional scale, local communities are linked by the dispersal of potentially interacting species among local habitats [1]. Species dispersal links local and regional community dynamics (*i.e.*, metacommunity dynamics) and influences local population dynamics and community composition [1]. A better understanding of the dispersal process, and its eco-evolutionary drivers, is therefore crucial for understanding its influences on community dynamics at different landscape scales [2,3].

Theoretical and empirical studies have demonstrated that dispersal depends on the experienced and anticipated biotic and abiotic environment, referred to as context-dependent dispersal [4–6]. Indeed, organisms do not move randomly through a landscape, the propensity, direction, and distance moved can be plastically adjusted to the local abiotic and biotic conditions encountered before and while moving [4]. Theory shows that individuals can disperse adaptively as emigration and immigration could depend on the expected fitness in the arrival patch available for colonization relative to the fitness expected in the departure patch [7]. Theory also predicts that such context-dependent dispersal can evolve in spatially and temporally heterogeneous habitats [8]. Further, the evolution of context-dependent dispersal depends on the reliability and cost of information acquisition [9]. Among the many factors theoretically found to drive the evolution of context-dependent dispersal are patch size and quality, and fluctuation in population density or kin competition [8,10,11]. Such context-dependent dispersal can itself affect eco-evolutionary dynamics, including source-sink population dynamics or species ranges, and can further affect metacommunity functioning and stability through changes in species abundances and community composition [12].

The direction and strength of local interactions are major determinants of fitness and therefore expected to be among the most important proximal drivers of dispersal [3]. Bottom-up and top-down controls of dispersal are now well documented (*e.g.*, [13]) and evidence is accumulating for the context-dependency of dispersal in other types of species interactions (*e.g.*, interspecific competition, host-symbiont interactions [14,15]). Further, certain species

can only disperse through other species' movements, such as animal-dispersed seeds or symbionts dispersing through their hosts' movements [16,17]. Despite the importance of species interactions, it remains unclear how their nature actually shapes dispersal plasticity within and among taxonomic groups. After a systematic review of the existing literature, we performed a meta-analysis of published studies investigating species interactions as proximal drivers of dispersal to discuss the potential consequences for metacommunity dynamics and identify important research gaps with respect to the development of a more mechanistic metacommunity theory. To do so, we extracted data from 118 observational and experimental studies focusing on either the emigration stage, the transience stage or the full dispersal process from emigration to immigration, excluding studies focusing only on colonisation. We focused on mobile and actively dispersing species, and thus excluded studies on sessile or passive dispersing species (*e.g.*, plants). Our database, which was taxonomically biased towards animals (essentially arthropods and vertebrates), encompassed 221 species pairs and six types of interactions experienced by the focal species, *i.e.*, detrimental interactions with predators, consumers or parasites, and beneficial interactions with resources, hosts or mutualists. We quantified how the presence/absence or the abundance of an interacting species influenced the dispersal of a focal species through plastic changes across interaction types, and identified key moderators of this context-dependent dispersal (Fig. 1). We especially addressed the following questions:

### Does the impact of interacting species on dispersal depend on the nature of species interactions?

Species interactions can be first described through their general effects on the focal species (Fig. 1). Beneficial interactors are resources, hosts, and mutualists that should increase the fitness of the focal species. Detrimental interactors are predators, parasites, and competitors that should decrease the fitness of the focal species. If dispersal depends on fitness expectations [7], detrimental interactions, endured or expected, should increase species dispersal propensity away from local habitats containing the interactor while the opposite should be true for beneficial interactions, even if this effect should depend on species ecological traits (see below). Evolution of such interaction-dependent dispersal has been theoretically and empirically shown for predator-prey, host-parasite, and interspecific competition interactions [6,14,18], showing for example that

models of density-dependent dispersal could be transferred from a single species to a multispecies context [14].

Beyond their expected effects on fitness, different species interactions might actually lead to different dispersal strategies to mitigate fitness effects (Fig. 1). Some interaction types might not be efficiently mitigated by species movements or might induce high dispersal costs. Dispersing away from local habitats might therefore fail to improve expected fitness. For example, interspecific competition negatively affects a competitor's fitness by reducing acquired energy, thus increasing the reward to move while reducing the energy available for movement. Thus, it may result in more complex - quadratic or threshold-like - relationships between the expected fitness consequences of interactions, the actual strength of interactions, and emigration propensity. Such relationships may vary with energy availability, movement costs and niche overlap between interacting species. Complex effects of competition have been found for intraspecific competition, with a systematic review showing that intraspecific density could either positively, negatively or non-linearly affect dispersal [19]. Predation risk on the other hand intrinsically reduces prey fitness, making movement out of habitats highly rewarding but also often highly risky [20], with potentially opposite effects on dispersal depending on the risk level. Similarly, by diverting their hosts' resources, parasites can constrain their dispersal [21]. However, hosts may increase their dispersal propensity to escape an infested habitat [15], and parasites themselves can manipulate their host's dispersal to increase contact rate and the transmission of parasites [21]. We expect the type of interactions to modulate the dependency of dispersal on interaction strength (*i.e.*, interaction-dependent dispersal) and this effect should further depend on a suite of biological and ecological factors (Fig. 1).

### Does the dispersal response depend on the spatiotemporal dynamics of interacting species?

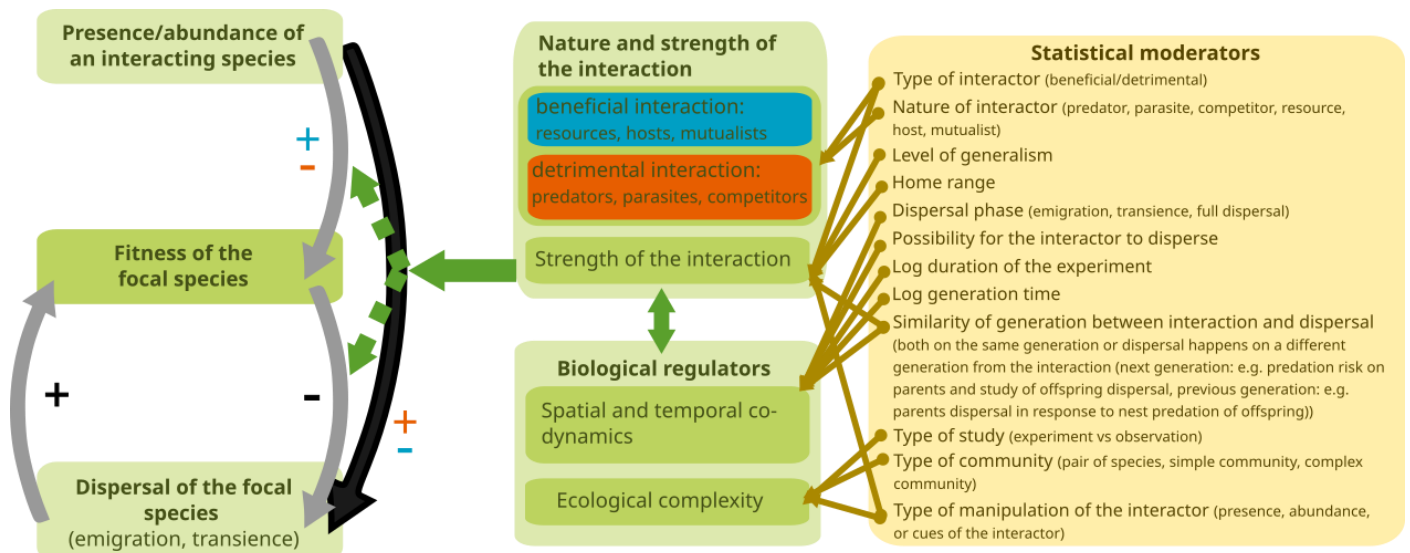
Dispersal is not always the best strategy to escape adverse interactions or to search for beneficial ones. Its efficiency should depend on temporal synchrony and spatial overlap of interacting species ([6], Fig. 1). First, dispersing may not lead to changes in encounters with an interacting species if that species has a wider spatial distribution. In such a case, dispersing individuals would bear more of the energy, time, and opportunity costs of moving [22] than its benefits. For example, predators often have larger home and movement ranges than their prey [23,24], but are also found at

lower densities. Prey species may thus need to disperse over longer distances to reduce predation risk. However, transience is a highly vulnerable stage when prey are exposed to predators [20], which may result in predators having different impacts on the focal prey species' emigration phase or transience depending on the spatiotemporal dynamics [13] and the asymmetry in space use between predator and prey. When dispersal does not efficiently influence the adverse or beneficial effects of interactions, species may opt for alternative mitigation strategies, such as switching their activity period or their microhabitat use. We first compared studies investigating interaction-dependent emigration (through emigration rate) and transience (through dispersal distance) for the different types of interactions. We expected interacting species to influence dispersal distances more than emigration probability when interacting partners differ in their spatial distribution (*e.g.*, consumer-resource interaction). Following the same rationale, we expected stronger influences of an interaction in (typically experimental) studies when only the focal species could disperse compared with cases where both species could disperse. Furthermore, we expected the relative home range of interacting species to affect the dispersal response (Fig. 1).

Second, the temporal dynamics of interacting species may modulate the efficiency of dispersal in mitigating species interactions. Interacting species may differ in 1) the daily and seasonal profiles of activity and 2) in the temporal autocorrelation of their population sizes [13]. For instance, in aphids, the evolution of delayed predator-induced dispersal, where predator presence induces the production of winged offspring, depends on the temporal correlation in predation risk [6]. We were not able to gather information on the daily and seasonal profiles of activity, but we investigated this temporal aspect by comparing studies in which the encounter with the interacting species and the dispersal responses occur within the same generation or across different generations, as well as studying the impact of the duration of the experiment and of species' generation time (Fig. 1).

### Do the interaction strength and ecological complexity affect the dispersal response?

One species' impact on the dispersal of another interacting species may depend on their interaction strength [14], as interaction strengths should affect fitness expectations. Assessing interaction strength between species is a non-trivial endeavour, both for the researcher [25], and possibly for the interacting organisms, which may rely on several types of cues to determine it. The interaction strength perceived by a



**Figure 1: The relationships between species interactions and dispersal**

The dispersal of a focal species depends upon its biotic context, especially if the presence/abundance of an interacting species affects its fitness (grey arrows). In this meta-analysis, we extracted data from the literature to determine how the presence/abundance of the interacting species affects the dispersal of a focal species (black arrow). The relationship between interacting species' presence/abundance and dispersal depends on the nature and strength of the biological interactors. Detrimental interactors such as predators, parasites or competitors (in red) negatively affect the fitness of the focal species (red – sign on the grey arrow). Because there is a negative relationship between fitness and dispersal (black – sign on the grey arrow), they should thus positively affect its dispersal (red + sign on the black arrow). On the other hand, beneficial interactors such as resources, hosts and mutualists (in blue) should positively affect the fitness (blue + sign on the grey arrow), and through the negative link between fitness and dispersal (black – sign), negatively affect dispersal (blue – sign on the black arrow). The effect of these interactions should depend on numerous biological regulators, related to the spatiotemporal co-dynamics and the ecological complexity, which affect the strength of interaction between species and thus the strength of interaction-dependent dispersal (green arrows). We translated these biological regulators into a number of statistical moderators (gold arrows) to explain the dependency of dispersal to the presence of an interacting species. By testing for these moderator effects on the relationship between the presence/abundance of the interacting species and dispersal of the focal species (gold and green arrows), we attempted to make inferences about the way fitness is affected by the interacting species and the way it affects the dispersal of the focal species (green arrows).

given individual may depend on various moderators including the abundances of the interacting partners, the actual presence or the perception of cues, the niche overlap and generalism of interacting partners, as well as the overall ecological complexity. For example, we can expect cues of the presence of interacting species to elicit a weaker perception of interaction strength and a weaker dispersal response than the actual presence of the interactor. Conversely, the fear of predators has long been considered to have stronger impacts on prey than their actual presence and consumption [26]. The effect of an interaction on species fitness and dispersal may further depend on community complexity (Fig. 1), *i.e.*, the diversity of interacting partners within the same and across interaction types. Multiple host species for a single parasite may for example decrease the interaction strength with each host species through a dilution effect that decreases disease risk [27]. A similar prediction can be made for any interaction type.

Comparing studies using a two- or a multi-species network may therefore provide information on the role of interaction strength, with the prediction that a design with pairs of species may overestimate the dependency of dispersal on interaction strength. Similarly, experimental studies may reduce ecological complexity, but have better detection of interaction strength, than observational studies. The strength of interaction may also depend on the level of generalism of interacting species, with more specialist interactors likely having stronger impacts on the focal species and hence their dispersal. Most of the studies investigating interaction-dependent dispersal lacked an assessment of interaction strength between species; however, several aspects of the environmental context could be used as a cue of interaction strength. We thus investigated modulating effects of metrics related to community complexity, types of manipulation (*i.e.*, cues vs. actual presence or abundance of interacting species), type of studies (observational vs.



experimental) and level of generalism of both the focal and interacting species in dispersal studies. Further, we used a second literature search to estimate expected interaction strengths between pairs of species present in our database, which was possible for a majority of species pairs but involved a large variation between the ecological contexts of dispersal and interaction strength studies.

## METHODS

### Systematic literature review

We compiled a database of existing studies quantifying how the presence/absence or the abundance of an interacting species influences the dispersal of a focal species. Our database focused on actively dispersing species to examine the relationship between the dispersal response and the interaction strength, but not the numerical and behavioural effects of dispersal vectors. We defined active dispersal as dispersal in which the organism either actively moves during the transience phase, or actively initiates the emigration phase (*e.g.*, ballooning dispersal in which the wind is the vector of the transience, but the organism actively initiates dispersal by its tiptoeing behaviour [28], or dispersal by a biological vector where the organism actively climbs on top of the vector [29]). Organisms that are passively picked up and carried by the wind or a dispersal vector, such as most cases of seed dispersal, were thus excluded. In addition, we excluded studies that focused only on the immigration/colonization phase of dispersal, because the habitat choices of focal species depending on local interactors (the purpose of the present study) could not be distinguished from the viability of focal species depending on local interactors (*i.e.*, colonization success). However, immigration decisions with respect to species interaction are expected to mirror emigration decisions and so we expect our conclusions to apply to immigration decisions as well [5]. In the end, our literature search included emigration decisions, dispersal distance, the timing of dispersal, and any type of species interactions (interspecific competition, consumer-resource interactions, parasitism, and mutualism). Fig. S1 shows the process of study identification, selection and the data extracted from each relevant article. We aimed at following the preferred reporting items for systematic reviews and meta-analyses (PRISMA, [30]) as well as its extension for ecology and evolutionary biology [31].

We conducted the literature search on Web of Knowledge in October 2021 (timespan: 1975-2021) including keywords for 1) dispersal in the title (dispers\* OR migrat\* OR emigrat\* OR immigrat\* OR colonis\* OR coloniz\* OR nomadi\*) and excluding other types of

movements, *i.e.*, seasonal migration (fall, autumn, spring migration, vertical migration, catadrom\*, anadrom\*), human migrations (*i.e.*, refugees, international migration, domestic migration, human migration, asylum, illegal), or particle dispersion, and 2) species interaction in the title and/or subject (predat\* OR resource\* OR prey\* OR parasit\* OR host\* OR compet\* OR facilitat\* OR mutualis\* OR cooperat\* OR phore\* OR commensal\* OR interspeci\* OR heterospeci\* OR context\* OR condition\* OR metacommunit\* OR "mutual inhibition" OR ammensalis\* OR symbio\*). We focused on the Web of Science core collection, and filtered results by Web of Science categories relevant to our broad thematic, see supplementary Box S1 for a full description of the keywords and categories. During the search process, we checked for the inclusion of known relevant articles in the database to ensure that we did not miss important articles. The search yielded 21,499 articles.

### Inclusion criteria

We examined each title and abstract to determine whether articles met the criteria for inclusion in our overview of the literature with the *metagear* package v0.7 [32] in R. Criteria for inclusion comprised (a) the presence, abundance or density of an interacting species was quantified and varied experimentally or in observational studies, (b) the rate of emigration or the dispersal distance or another dispersal metric of a focal species that was quantified in different contexts of species interactions, (c) the effect of a single interacting species on a focal species can be isolated when more than two species were studied and (d) the two species were interacting species in natural environments, excluding artificial biotic elements (*e.g.*, unnatural resource or predator species). At times, the title and abstract were too vague to positively assess these three criteria of inclusion, and the articles were kept for further detailed reading of the text; they could be thus excluded in a second filtering session. All examiners went through a training process in which they screened abstracts and titles for a set of 150 articles that were pre-selected by the first author to contain studies both easy and more difficult to rate as relevant or irrelevant. We estimated the inter-examiner accuracy, yielding a Cohen's Kappa of 0.40, corresponding to a fair to moderate agreement [33]. This first batch allowed to identify points of misunderstanding and better explain the criteria to select an article. Then, all examiners went through 70 new articles that were deemed especially difficult to rate and we checked for potential discrepancies. Although the batch was more difficult, inter-examiner accuracy went up ( $K = 0.43$ ). This second batch allowed us to clarify the final difficult points before splitting the

abstracts between examiners so that each examiner read and rated ~1100 abstracts. During this second phase, inter-examiner accuracy was examined again on 20 articles per reviewer, yielding a K of 0.73, considered a substantial agreement [33]. The filtering process led to a selection of 1,539 studies from the original search that fitted the scope of this overview.

### Effect size extraction

Selected articles were reviewed in full to determine whether they fit our inclusion criteria, contained relevant data, and whether the results were presented with sufficient clarity to extract effect sizes (Fig S1). During this step, we excluded (a) studies in which the focal species dispersed passively and in which there was no active choice to emigrate, (b) studies focused on the colonisation process only, keeping studies on emigration, transience, or the ones monitoring the full dispersal process, (c) studies in which the second species did not interact with the focal species, (d) studies in which the effect of an interacting species on the dispersal of the focal species was compared to a control with a second interacting species instead of no interacting species or different abundances of interacting species. This step led to the further exclusion of 1,420 articles from the first search. In the final set of 119 studies, we extracted 403 effect sizes and collected information on several moderators to investigate our questions of interest (See supplementary reference list). Data to calculate effect sizes were extracted preferentially from raw data when available, from figures using the *juicr v 0.1* R package, or directly from the paper (tables or main text). Effect sizes were calculated with *esc v0.5.1* and *effectsize v0.8.5* R packages, and computed as Hedges' *d* from pairs of means (282 effect sizes, es), or converted to Hedges' *d* from contingency tables (41 es), correlations (15 es), log odds ratios (19 es), from different test metrics reported in the text (46 es, calculated from  $\chi^2$ , *F* or *t* values, non-parametric test values, or partial  $\eta^2$  from ANOVA-like tables), see references [34–40] and Table S1 for a list of equations used. Depending on the study, the sign of the effect sizes had to be reversed to be comparable among studies (e.g., effect sizes of remaining rate instead of departure rate, time to dispersal where increased time suggests decreased dispersal propensity). When studies presented several effect sizes for the same dispersal metric, e.g., when the impact of the interacting species was crossed with the effect of another biotic or abiotic factor, we combined groups following [35] when there was no significant interaction between the effect of species interaction and the second factor. Several effect sizes were missing variance information (*n* = 16), thus we used an imputation procedure to fill-in back-

transformed variance from the predicted values from a model of log(variance) by log(study sample size). Further, several effect sizes had an extremely large variance (*n* = 6 es with variance > 2) which led to instability in meta-analysis results, and we decided to drop these effect sizes, leading to a final sample size of 397 effect sizes from 118 studies (exclusion of one study).

Aside from the effect sizes, we extracted several aspects of the experimental design (Table S2). First, we included the taxonomic identity for the focal taxon and interacting taxon, i.e., either the species or the taxonomic level described (e.g., genus, family, order; for simplicity we will refer to the focal species and interacting species throughout the text, but higher taxonomic levels may be used depending on the study, Table S2). Second, we added the type of interactor, i.e., whether the interacting species is a detrimental interactor such as a predator, resource, competitor, or a beneficial interactor such as a host, parasite, mutualist (see the details of each category in Table S2). Third, we detailed the dispersal phase studied (emigration, transience, or full dispersal process from emigration to settlement). Fourth, we included the type of manipulation (or variation in the case of observational studies) of the interactor: manipulation of presence vs. abundance, manipulation of actual physical presence vs. cues of presence, level of community complexity (pairs of species, simple community, complex community), possibility for the interactor to disperse during the experiment, similarity of generation for interaction and dispersal (same generation, or different generation, e.g., next generation for the effect of predation risk experienced by parents on offspring dispersal, or previous generation for the effect of nest predation risk on parent dispersal). Fifth, we added the type and characteristics of study: experimental vs. observational study, laboratory, semi-natural or field study, as well as the duration of the study in days.

In addition to the information extracted from the studies, we further searched within the literature for information on the focal species' generation time, the home range of the two interacting species [41–45] (unfortunately only found for 17 es), the level of generalism of the two interacting species (rated from 1 to 4 on whether they interact with only one species, with species from the same genus or family, with species from the same order, or with species from different orders), and interaction strengths between pairs of species (Table S2). These interaction strengths between pairs of species found in the database are given as standardized effects of the presence or

abundance of the interacting species on a fitness-related trait in the focal species (survival, fecundity, body condition, body growth, or abundance), found either directly in the screened articles (166 es) or in a larger literature search (191 es, interaction strength was missing for 40 es). A single author (JC) searched for the strength of interaction and was different from the author calculating effect sizes for interaction effects on dispersal (EB) to reduce, without fully preventing, biases in the estimation of strength and its covariation with dispersal response. There was also a large variation in the experimental conditions of dispersal and fitness-related traits studies, which should result in a more conservative approach. As we were unable to extract generation time for two taxa, we imputed the median generation time of their closest taxa in the database.

We used taxonomy as a proxy for phylogenetic relatedness, using the *taxize* package v0.9.100 to gather taxonomic information from the NCBI database. When the taxon considered was absent from the NCBI database, we used the GBIF or ITIS databases. We then calculated a taxonomic phylogenetic tree from the taxonomic data (kingdom-phylum-class-order-family-genus-species), and used Grafen's method of computing branch length [46] with the *ape* package v 5.1-1 (Fig S2).

## Statistical analyses

We studied the impact of interacting species on dispersal through multilevel mixed effects meta-analytic models via the *rma.mv* function of the *metafor* v 4.2-0 package [47] in R v4.3.1. We used a model selection approach to investigate our questions, thus the global model contains moderators for all questions of interest.

In a first step, we investigated whether the type of interactor [*i.e.*, beneficial interactor (resource, host and mutualist) vs. detrimental interactor (predator, competitor and parasite)] interacted with our moderators of interest to drive dispersal response to interacting species presence or abundance (Fig. 1). To do so, we ran a full model with:

- all pairwise interaction between the type of interactor (beneficial/detrimental) and the dispersal phase, the level of generalism of the focal species, the level of generalism of the interactor, the type of manipulation of the interacting species, the level of community complexity, the possibility for the interacting species to disperse, the similarity in generation between the interaction and dispersal phase, the type of study (observational vs. experimental), the centered log

duration of the experiment, and the centered log generation time of the focal species as moderators of interest, and

- the study ID, the focal species ID, the focal species shared phylogenetic relatedness (branch length from the taxonomic phylogenetic tree), and the interacting species ID as random effects (see Box S2 for the full model equation).

We then used the dredge function from the *MuMIn* v 1.47.5 package to select models with the best fixed structure, and averaged models within  $\Delta AIC_c < 2$ . We calculated the averaged conditional estimates from this model with the sum of weights of the metric across the models (SW, aka relative importance). We further refitted a model using all of the moderators present in the averaged best model to assess heterogeneity to confirm sources of variance across the dataset and computed the heterogeneity statistics  $I^2$  at each level, corresponding to the ratio of true heterogeneity to total observed variation. To understand whether there was publication bias, we visualized effect sizes using funnel plots of the residuals of this model, and calculated Rosenberg's fail-safe number [48], which estimates the number of missing values averaging a  $z$ -value of zero needed to make effect sizes statistically insignificant. Third, we ran Egger's regressions using the meta-analytic residuals as the response variable, and the precision (defined as the square root of the inverse of variance) as the moderator. Intercepts of this regression that do not overlap zero are evidence of publication bias [49]. Finally, we analysed temporal trends in effect sizes that could indicate time-lag bias [49] by adding the interaction between time and the consequence of the interaction on fitness to the model containing all moderators present in the best model.

In a second step, we assessed the effects of moderators for beneficial and detrimental interactions separately because the effect sizes of their effects on dispersal are of opposite signs (*i.e.*, beneficial interactions reduce dispersal propensity while detrimental interactions increase it). We divided the dataset into beneficial and detrimental interactors, and for each data subset, we fitted a full model with the same random effects as the above model and the exact nature of the interaction (*i.e.*, resource, host and mutualist for the beneficial interactors subset and predator, parasite and competitor for the detrimental interactors subset), the dispersal phase, the level of generalism of the focal species, the level of generalism of the interactor, the type of manipulation of the interacting species, the level of community complexity, the possibility for the interacting species to disperse,



the similarity in generation between the interaction and dispersal phase, the type of study (observational vs experimental), the centered log duration of the experiment, and the centered log generation time of the focal species as moderators of interest (Box S2). We used the same model selection and model averaging procedure as above to select the best averaged model. We further refitted models using all of the moderators present in the averaged best models to assess heterogeneity, study publication bias, and finally plot results by moderator. We used the *emmeans* package v1.8.8 to calculate the overall adjusted effects, as well as the estimated marginal means for different levels of each moderator.

Lastly, because we were unable to gather home range and interaction strength information for most pairs of species, we ran two separate analyses for these two questions on the subset of studies for which we had information (7 studies with 17 effect sizes for home range, 108 studies with 357 effect sizes for interaction strength). Models used the study ID, focal species ID, and interactor ID as random effects and either the centered log ratio of home ranges between the focal species and the interactor or the interaction strength as a fixed moderator.

## RESULTS

### Summary of the dataset

We identified 118 studies that met our inclusion criteria with 397 effect sizes for 144 focal species and 165 interacting species. Focal species spanned a wide range of taxa, with Arthropoda being the most represented (236 effect sizes), followed by Chordata (70) and Ciliophora (47), and then Nematoda, Mollusca, Annelida, and Cryptophora (Fig. S2-S3). As we restricted our search to actively dispersing species, plants were excluded. Our database further reflected a taxonomic bias in dispersal publications, with the number of effect sizes per taxonomic group significantly deviating from the frequencies expected from the diversity of species in the Catalogue of Life [50,51] through the recorded number of species in each group ( $\chi^2 = 354$ ,  $df = 4$ ,  $p < 2e16$ , Table S3). Specifically, Chromista were overrepresented, and among Animalia, Arthropoda represented 68 % of our effect sizes but were still underrepresented (83 % under the null expectation) and Chordata were overrepresented (20 % of observed effect sizes compared to 5 % expected, Table S3). Such overrepresentation of Chordata is common in ecological studies, and the magnitude of overrepresentation is much less in our database than in behavioural studies for instance, where Chordata

represent up to 71% of publications [50]. The database included 152 effect sizes for interactions with beneficial interactors including resources (125), mutualists (21), and hosts (6), and 245 effect sizes for interactions with detrimental interactors including predators (116), competitors (73), and parasites (56). Studies also varied for the dispersal phase considered, with 275 considering emigration, 48 transience, and 74 monitoring the full dispersal process, as well as for the method to manipulate the interacting species (actual presence or absence of interacting species, varying abundance, or cues of presence; see Fig. S3-S4 and Table S2 for a further exploration of the moderators).

### Description of the models and publication bias

We first studied how the type of interactor (beneficial vs. detrimental interactor) and moderators affected the context-dependency of dispersal on species interactions using the full dataset. Our averaged best model included several pairwise interactions between the type of interactor (beneficial or detrimental) and the dispersal phase (emigration, transience, or full dispersal), the type of study, the duration of the study, and with other moderators having weaker effects (Table 1). This model found important heterogeneity among studies ( $I^2_{\text{study}} = 63.2\%$ ), as well as some heterogeneity related to the focal species' identity ( $I^2_{\text{focal}} = 8.3\%$ ), phylogeny ( $I^2_{\text{focal}} = 8.3\%$ ) and interactor's identity ( $I^2_{\text{interactor}} = 16.8\%$ ), for a total heterogeneity of  $I^2 = 96.7\%$ . Such high heterogeneity is expected in ecology and evolution meta-analyses, with the mean heterogeneity being 91.7 % [52]. Funnel plots, Egger's test and the Rosenberg fail-safe number showed no significant publication bias; funnel plots did not reveal significant asymmetry (Fig. S5), Egger's test showed an intercept that crossed zero for the residuals intercept (estimate [95% CI] = 0.13 [-0.03, 0.28],  $t = 1.6$ ,  $df = 395$ ,  $p = 0.119$ ), and the Rosenberg fail-safe number was very high ( $N = 47,929$ ). Additionally, we found that the effect size changed over time, suggesting a time-lag effect that was only present for beneficial interactors (Table S4).

In a second step, we split the dataset according to the previously defined beneficial and detrimental interactor types, replacing these broad types with the exact nature of the interaction (predators, parasites, competitors, resources, hosts, or mutualist) as a moderator on the two data subsets. The two analyses did not retain the same moderators, suggesting that the importance of a moderator depended on the broad type of interaction (Table 2, see below for description). Both models showed important heterogeneity ( $I^2 = 93.9$  vs. 95.5 % respectively for beneficial vs.

detrimental interactions), but the distribution of the heterogeneity varied to a large extent among datasets, with a more important among-study effect for beneficial interactions ( $I^2_{\text{study}} = 88.0$  vs 45.8 %), and a larger importance of species identity and species phylogeny for detrimental interactions ( $I^2_{\text{focal}} = 2.6$  vs 13.8 %,  $I^2_{\text{phylo}} = 2.6$  vs 13.8 % and  $I^2_{\text{interactor}} = 0.7$  vs 22.1%). When looking at the publication bias of those models with funnel plots and Egger's test, we found some asymmetry for the detrimental interaction dataset (Fig. S6, Egger's test intercept [95% CI] = 0.30 [0.11, 0.48],  $t = 3.2$ ,  $df = 243$ ,  $p = 0.002$ , Rosenberg fail-safe  $N = 30,695$ ), suggesting some publication bias, but not for the beneficial interaction dataset (Fig S6, Egger's test intercept [95% CI] = -0.21 [-0.64, 0.22],  $t = -0.98$ ,  $df = 150$ ,  $p = 0.33$ , Rosenberg fail-safe  $N = 17,746$ ).

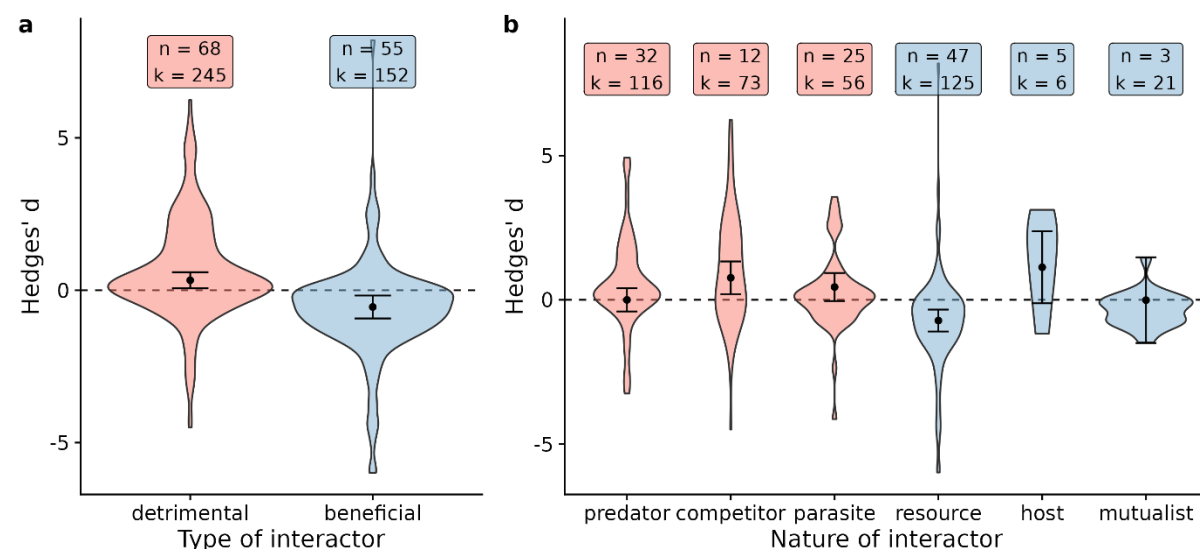
## Does the impact of interacting species on dispersal depend on the nature of species interactions?

Our global model found that the type of interactor and its interaction with various moderators affected the dispersal response to interacting species (Table 1). Overall, the marginal effect size of this global model crossed zero (-0.029 [-0.267, 0.209] adjusted effect [95%CI]), which was explained by the mix of decreasing and increasing effects on the dispersal of beneficial and detrimental interactions (Table 1). When we divided the dataset into beneficial and detrimental interactors, dispersal propensity indeed decreased (adjusted effect: -0.55 [-0.92, -0.17]) and increased (adjusted effect: 0.33 [0.06, 0.59]) respectively when beneficial interactors and detrimental interactors were present or more abundant (Fig. 2a).

**Table 1: Summary from the averaged best model investigating the effect of moderators on impacts of interacting species on focal species dispersal**

*The results are issued from a model selection from a full model described in Box S2, averaging estimates from models where  $\Delta AIC_c < 2$ . The results show the conditional averaged estimates and SE, z and p-values, as well as the sum of weights of the moderator (SW).*

Moderator	Level	Estimate	SE	z-value	p-value	SW
Intercept		-0.36	0.19	1.94	0.053.	
Dispersal phase	full dispersal	0.03	0.23	0.12	0.902	1.00
	<b>transience</b>	<b>-1.30</b>	<b>0.36</b>	<b>3.64</b>	<b>&lt;0.001***</b>	<b>1.00</b>
Centered log duration		<b>-0.13</b>	<b>0.04</b>	<b>3.28</b>	<b>0.001**</b>	<b>1.00</b>
Centered level of generalism focal species		<b>0.23</b>	<b>0.11</b>	<b>2.09</b>	<b>0.037*</b>	<b>1.00</b>
Type of community	<b>simple community</b>	<b>0.89</b>	<b>0.24</b>	<b>3.69</b>	<b>&lt;0.001***</b>	<b>1.00</b>
	<b>complex community</b>	<b>0.73</b>	<b>0.29</b>	<b>2.51</b>	<b>0.012*</b>	<b>1.00</b>
Type of interactor	beneficial	-0.29	0.20	1.46	0.145	1.00
Type of study	observation	0.16	0.31	0.53	0.597	1.00
Type of interactor:Dispersal phase	beneficial:full dispersal	0.58	0.36	1.61	0.107	1.00
	<b>beneficial :transience</b>	<b>1.39</b>	<b>0.42</b>	<b>3.27</b>	<b>0.001**</b>	<b>1.00</b>
Type of interactor:Centered log duration	<b>beneficial</b>	<b>0.23</b>	<b>0.06</b>	<b>3.83</b>	<b>&lt;0.001***</b>	<b>1.00</b>
Type of interactor:Type of study	<b>beneficial:observation</b>	<b>-1.44</b>	<b>0.52</b>	<b>2.75</b>	<b>0.006**</b>	<b>1.00</b>
Centered level of generalism interactor		<b>-0.21</b>	<b>0.11</b>	<b>2.02</b>	<b>0.044*</b>	<b>0.92</b>
Type of manipulation of interactor	abundance	-0.14	0.11	1.33	0.185	0.69
	cues of presence	0.28	0.18	1.50	0.134	0.69
Centered log generation time		0.06	0.04	1.28	0.200	0.31
Type of interactor:Centered log generation time	beneficial	-0.09	0.06	1.60	0.109	0.20
Similarity generation dispersal-interaction	different generation	0.26	0.29	0.90	0.369	0.17
Type of interactor:Centered level of generalism focal species	beneficial	0.12	0.17	0.67	0.505	0.08



**Figure 2: The effect of interacting species on dispersal of the focal species depends on the type of interactor**

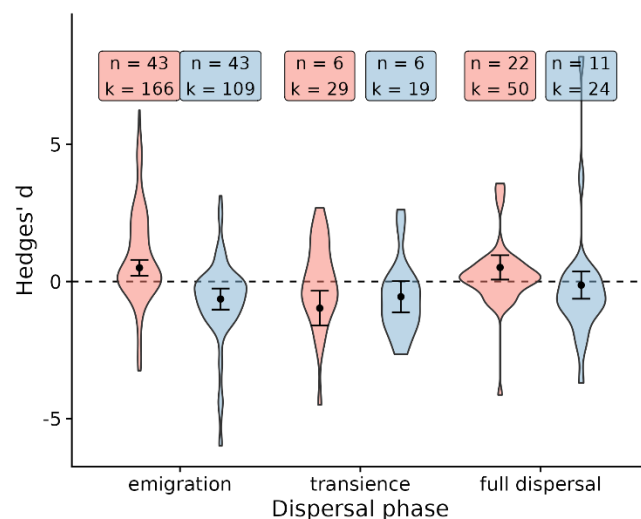
Effect of the (a) type of interactor (red: detrimental interactors, blue: beneficial interactors) and (b) the nature of interactor (predators, competitors, parasites, resources, hosts, mutualists) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with point and error bars corresponding to the marginal effect means and 95% CI from the two meta-analytic models for the subsets (i.e., beneficial and detrimental interactions, Table 2, Table S5), and labels corresponding to the number of effect sizes across categorical moderators (k) and the number of studies across moderators (n).

The exact nature of the beneficial interactor (i.e., resources, hosts, or mutualist) had an important effect on dispersal propensity (SW = 0.83), while the nature of the detrimental interactor (i.e., predators, parasites or competitors) had only weak effects (SW = 0.15, Table 2). While beneficial interactions generally reduced dispersal propensity, parasites tended to increase their dispersal propensity when their host was present or more abundant (Table 2, Table S5, Fig. 2b). On the contrary, all detrimental interactions had similar effects on dispersal, with competitors tending to have a stronger effect (Table 2, Table S5, Fig. 2b).

### Does the dispersal response depend on the spatiotemporal dynamics of interacting species?

Moderators related to spatiotemporal dynamics influenced the strength of interaction-dependent dispersal. In the full dataset, the interactions between the type of interactors and the dispersal phase had a strong impact on dispersal (SW = 1, Table 1). This was confirmed with data subsets on beneficial and detrimental interactors (SW ≥ 0.91, Table 2). The presence or abundance of detrimental interactors increased the rates of emigration and full dispersal while it decreased dispersal distance (i.e., transience phase, Fig. 3, Table S5). Beneficial interactions had a stronger negative effect on dispersal propensity at the

emigration phase than for the transience phase and the full dispersal process (Fig. 3, Table S5).



**Figure 3: The effect of interactors on focal species dispersal varies depending on the dispersal phase considered**

Effect of the dispersal phase and the type of interactor (red: detrimental interactors, i.e. predators, competitors, parasites, blue: beneficial interactors, i.e. resources, hosts, mutualists) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with point and error bars corresponding to

the marginal effect means and 95% CI from the two meta-analytic models for the subsets (i.e., beneficial and detrimental interactions, Table 2, Table S5), and

labels corresponding to the number of effect sizes across categorical moderators ( $k$ ) and the number of studies across moderators ( $n$ ).

**Table 2: Summary from the averaged best model investigating the effect of moderators on impacts of interacting species on focal species dispersal subsetting the data by type of interactor**

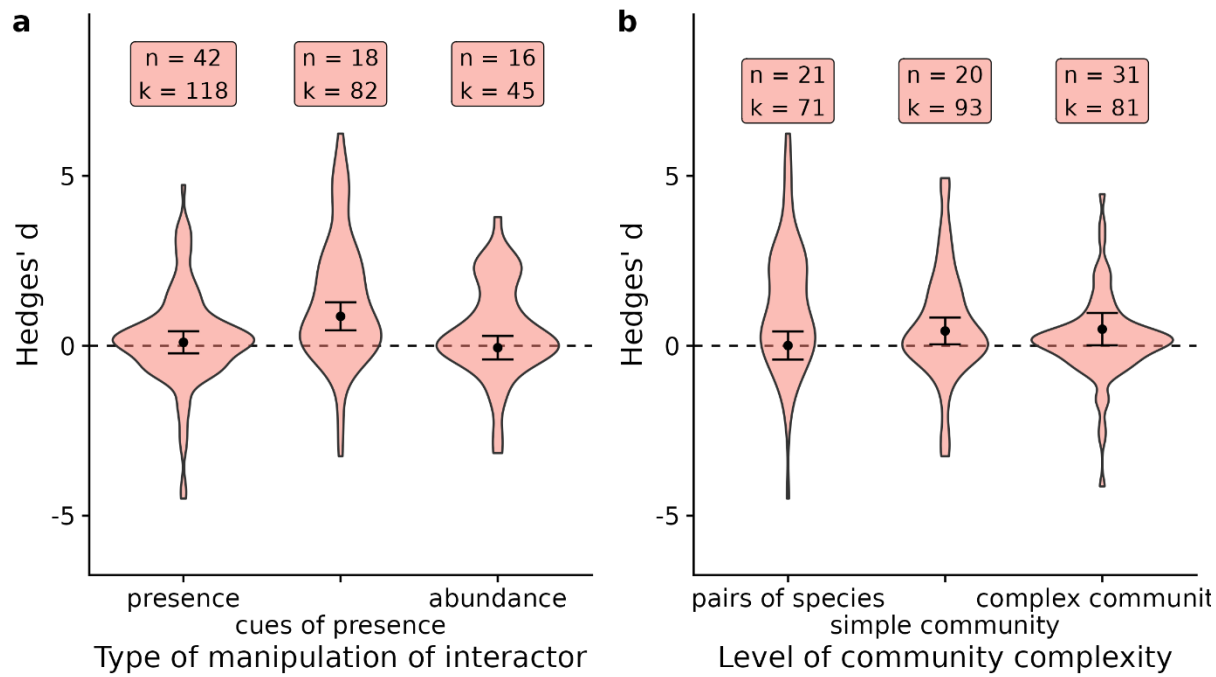
The results are issued from a model selection from a full model, averaging estimates from models where  $\Delta AIC_c < 2$ . The results show the conditional averaged estimates and SE,  $z$  and  $p$ -values, as well as the sum of weights of the moderator (SW).

Data subset	Moderator	Level	Estimate	SE	$z$ -value	$p$ -value	SW
Detrimental	Intercept		-0.12	0.24	0.51	0.610	
	Dispersal phase	full dispersal	0.06	0.22	0.28	0.780	1.00
		<b>transience</b>	<b>-1.18</b>	<b>0.34</b>	<b>3.49</b>	<b>&lt;0.001***</b>	1.00
	<b>Centered log duration</b>		<b>-0.12</b>	<b>0.04</b>	<b>2.77</b>	<b>0.006**</b>	1.00
	Type of manipulation of interactor	abundance	-0.17	0.13	1.29	0.196	1.00
		<b>cues of presence</b>	<b>0.58</b>	<b>0.25</b>	<b>2.36</b>	<b>0.018*</b>	1.00
	<b>Level of community complexity</b>	<b>simple community</b>	<b>0.54</b>	<b>0.26</b>	<b>2.12</b>	<b>0.034*</b>	0.78
		<b>complex community</b>	<b>0.69</b>	<b>0.28</b>	<b>2.43</b>	<b>0.015*</b>	0.78
	Centered level generalism focal		0.27	0.16	1.71	0.087.	0.70
	Centered level generalism interactor		-0.17	0.11	1.47	0.143	0.39
	Type of study	observation	0.42	0.30	1.40	0.161	0.25
	Centered log generation time		0.06	0.04	1.30	0.194	0.24
	Possibility for interactor to disperse	yes	0.31	0.28	1.13	0.256	0.21
	Similarity in generations between dispersal and interaction	different generation	0.54	0.38	1.43	0.154	0.20
	<b>Nature of interactor</b>	<b>competitor</b>	<b>0.76</b>	<b>0.37</b>	<b>2.04</b>	<b>0.041*</b>	0.15
Beneficial		parasite	0.49	0.32	1.55	0.121	0.15
	<b>Intercept</b>		<b>-0.71</b>	<b>0.22</b>	<b>3.29</b>	<b>&lt;0.001***</b>	
	<b>Dispersal phase</b>	<b>full dispersal</b>	<b>0.45</b>	<b>0.18</b>	<b>2.47</b>	<b>0.013*</b>	0.91
		transience	0.08	0.24	0.34	0.733	0.91
	<b>Nature of interactor</b>	<b>host</b>	<b>1.73</b>	<b>0.70</b>	<b>2.48</b>	<b>0.013*</b>	0.83
		mutualist	0.51	0.82	0.62	0.537	0.83
	Centered level generalism interactor		-0.46	0.26	1.80	0.072.	0.79
	Centered log duration		0.06	0.04	1.60	0.110	0.74
	Type of study	observation	-0.60	0.42	1.40	0.161	0.21
	Centered level generalism focal		0.13	0.14	0.94	0.345	0.10

In addition, longer experiments showed weaker effects of interactions on dispersal and this attenuation was stronger for detrimental than for beneficial interactions (Table 1 & 2, SW = 1 vs 0.74, resp., Fig. S7). The generation time of the focal species further had a very weak effect for detrimental interactions only, with a slightly stronger positive effect of detrimental interactors on dispersal for species with longer generation times (SW = 0.24, Table 2, Fig. S7).

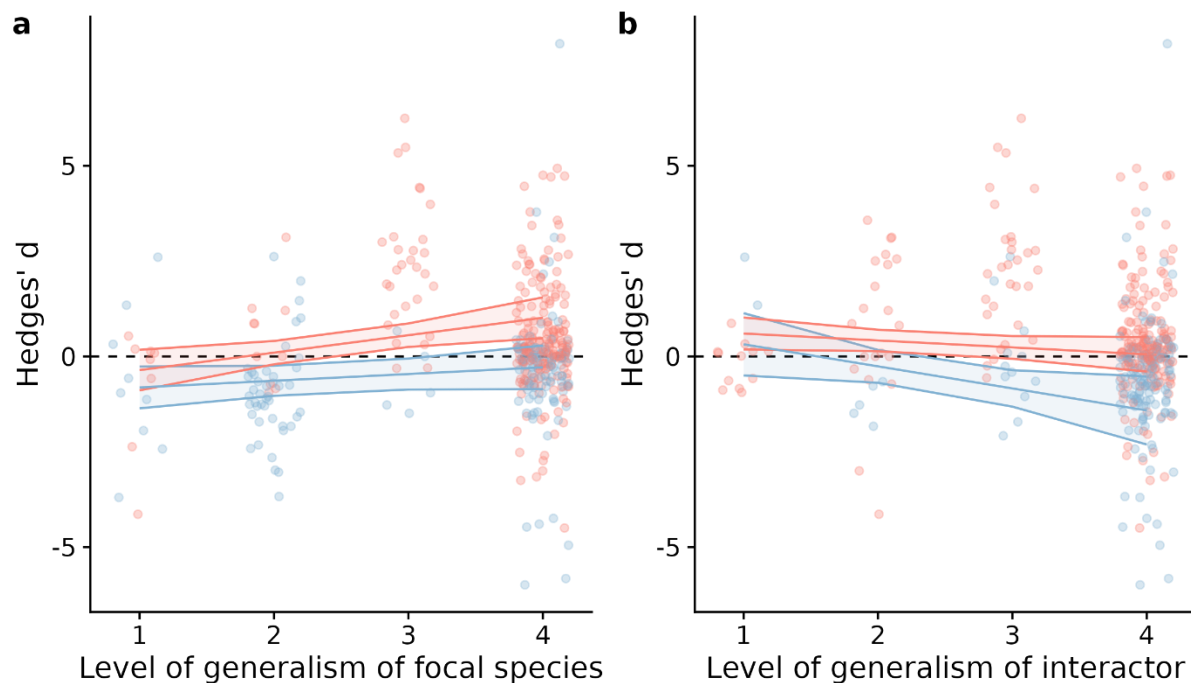
We found that increasing ratios of home ranges between the focal species and the interactor tended to decrease the positive effect of detrimental interactors on dispersal, although the effects are to be taken with caution due to the very low sample size (only 7 studies on detrimental interactions with 17 effect sizes, see Methods and Table S6).





**Figure 4: For detrimental interactions, the effect of interacting species on focal species dispersal varies depending on the biotic context**

Effect of (a) the type of manipulation of the interactor (i.e. presence, cues of presence or abundance) and (b) the level of community complexity (pairs of species, simple community, complex community) on the effect of detrimental interactors on dispersal (positive Hedges'  $d$  values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with point and error bars corresponding to the marginal effect means and 95% CI from the meta-analytic model for the detrimental interactors data subset (Table 2, Table S5), and labels corresponding to the number of effect sizes across categorical moderators ( $k$ ) and the number of studies across moderators ( $n$ ).



**Figure 5: The effect of interactors on focal species dispersal varies depending on both species' level of generalism**

Effect of the generalism of (a) the focal species or (b) the interactor and type of interactor (red: detrimental, blue: beneficial) on the effect of interacting species on dispersal (positive Hedges'  $d$  values: increased dispersal in the presence of interactors, negative: decreased dispersal). The level of generalism is rated from 1 to 4 on whether species

interact only with one species (1), with species from the same genus or family (2), with species from the same order (3), or with species from different orders (4). Points represent the effect sizes, and lines and confidence intervals are displayed from marginal means and 95 % CI from the two meta-analytic models calculated at the four levels of generalism.

### Do the interaction strength and ecological complexity affect the dispersal response?

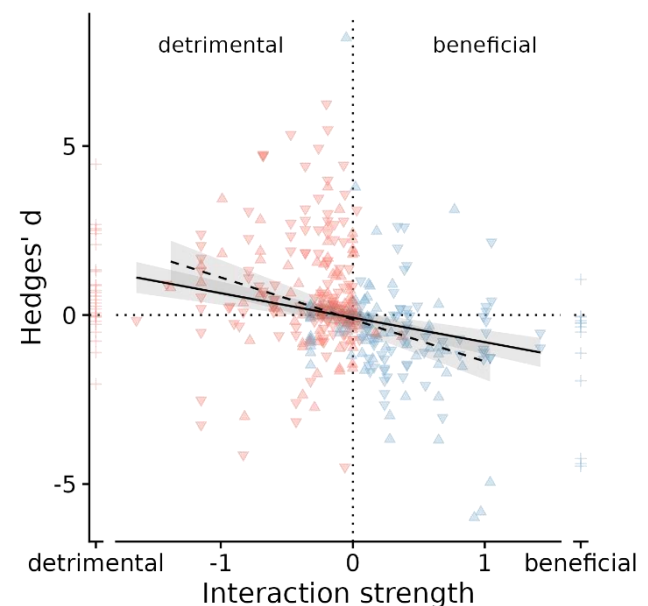
Moderators related to the perception of interaction strength by an individual and the ecological complexity influenced the strength of interaction-dependent dispersal. The full database showed a marked importance of the community complexity level ( $SW = 1$ ) and a weaker importance of the way the interactor was manipulated ( $SW = 0.69$ , Table 1). Subsetting by interactor types showed that these effects were mainly found for detrimental interactions ( $SW = 1$  and  $0.78$  resp. for community complexity level and type of manipulation, Table 2). More complex systems with three or more species or natural communities showed stronger positive effects (Fig. 4, Table S5), while manipulation of cues of presence showed stronger positive effects than manipulation of presence (Fig. 4, Table S5). Whether the study was experimental or observational was unlikely to have an effect ( $SW \leq 0.25$ , Table 2).

The level of generalism of both species was evidenced as important ( $SW \geq 0.92$ , Table 1). Subsetting beneficial and detrimental interactions showed that higher levels of generalism of the focal species led to slightly stronger positive effect of detrimental interactions on dispersal ( $SW = 0.70$ , Table 2, Fig. 5, Table S5) and more generalist beneficial interactors had slightly stronger negative effects on dispersal ( $SW = 0.79$ , Table 2, Fig. 5, Table S5).

The possibility for the interactor to disperse and the similarity of generation between interaction and dispersal were unlikely to have a strong effect on context-dependent dispersal ( $SW \leq 0.21$ , Table 2, Table S5).

We further gathered a continuous estimate of interaction strengths between pairs of species present in our database from the literature (193 pairs of species and 357 effect sizes). We found a strong negative relationship between measured interaction strength and dispersal response to interaction (Table S7, Fig. 6). While matching the effect of the binary interaction type (see above), this continuous interaction strength was a better predictor (Table S7, Fig. 6). When restricting this analysis to studies measuring concomitantly the dispersal response to interaction and the interaction strength (166 effect sizes), the impact of interaction strength was an even better

predictor (Table S7, Fig. 6).



**Figure 6: The effect of interactors on focal species dispersal varies on the strength of interaction between species**

*Effect of the interaction strength between pair of species and type of interactor (red: detrimental, blue: beneficial) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal), for the 357 effect sizes for which we could retrieve interaction strength. Coloured points represent interaction strength as a function of Hedges' d, for either the subset of data for which interaction strength was measured concomitantly to dispersal ("strict database", triangles, 166 es), for which the interaction strength was found in the secondary literature (upside-down triangles, 191 es), or for which the interaction strength was not found at all and thus is only categorized as positive or negative (crosses, 40 es). Lines and ribbons represent the effect of interaction strength on dispersal from the meta-analytic model, either on the strict database (dashed line, Table S7), or on all measures of interaction strength (full line, Table S7).*

## DISCUSSION

Species do not move randomly among habitats in a landscape [53]. On the contrary, a number of external cues about abiotic and biotic contexts, and internal cues about physiological states influence individuals'

decision to leave their habitats, to orient themselves in a landscape, and to settle in a novel habitat [4]. Context-dependent dispersal is now well-supported by accumulating empirical evidence and theoretically bolstered by the adaptive dispersal theory [5,7,13,19,54–58]. Accordingly, individuals should leave habitats with adverse conditions and search for better ones, as long as the energy, time, and risk barriers to dispersal (*i.e.*, dispersal costs) do not offset the benefit [22]. Using a systematic review approach, we investigated the relationship between species interactions, a key driver of dispersal suffering from an absence of global synthesis in the literature, and dispersal plasticity including all types of species interactions, across diverse taxonomic groups, focusing on actively dispersing organisms.

Our first main result is that the interaction-dependence of dispersal matches the expected fitness consequences of the interaction. The presence or abundance of detrimental interactors (consumers, parasites or competitors) increased the dispersal propensity of a focal species. Conversely, the presence or abundance of beneficial interactors like resources, hosts and mutualists, decreased the dispersal propensity of a focal species. While clearly fitting basic adaptive dispersal theory, there is a large variation around this general pattern that is explained by dependencies on the dispersal phase studied. We found that the impacts of detrimental interactions changed from positive to negative depending on whether the study focused on the emigration or transience phase, and we found that the dependencies on the duration of the experiment, on the complexity of the community studied, and on other moderators related to ecological complexity, interaction strength, and spatiotemporal dynamics.

We expected the context-dependency of dispersal to depend on the exact nature of the interaction, with for example responses to predators not being the same as responses to parasites due to *e.g.*, differences in the efficiency of dispersal to mitigate these detrimental interactions (see the introduction). This last result was only partially supported, with only weak differences between species responses to predators, parasites and competitors for detrimental interactions and a difference between responses to hosts and resources for beneficial interactions. This weak variation is likely not explained by a potential scarcity of studies involving predators, as the sample size per interaction is relatively high (32 studies and 117 effect sizes), competitors (12 studies and 73 es), and parasites (25 studies and 56 es). Similarly, the difference between responses to host and resource presence was

unexpected, although the sample size for hosts was very low. Consumers logically decreased their dispersal propensity away from places with available resources, while parasites tended to disperse away from habitats with more hosts. We posit that this surprising result may be explained by underlying positive effects of host occurrence on the population growth and dynamics of parasites leading to intertwined effects of inter- and intraspecific interactions. However, the number of studies investigating both inter- and intraspecific interactions and the population growth of interacting species was too limited [59] to test this hypothesis.

Similar to the reported effects of intraspecific density [19], we showed that the consequence of interspecific interactors' presence and abundance led to complex responses on dispersal. Species have been shown to respond to intraspecific density through emigration in diverse ways, with 30 % of the 145 studies reviewed showing no density-dependent dispersal, 36 % showing positive density-dependent dispersal, and 25 % negative density-dependent dispersal, with 9% representing nonlinear responses [19]. Our meta-analysis similarly showed important heterogeneity in dispersal responses to interspecific interactions which is not surprising given the dependency of interaction strength itself on biotic and abiotic context [60]. The strength of biotic interactions was shown to particularly vary along abiotic gradients, with spatial and temporal gradients showing lower variation, and to particularly vary in laboratory studies, while mesocosm and field studies showed lower variation [60]. Chamberlain and colleagues [60] even reported changes in the sign of the interaction across contexts within a study, with an important proportion of changes among mutualists and competitors. It is thus possible that context-dependent variation in the strength of biotic interactions, due to experimental design, abiotic or biotic variation, would in return lead to variation in the context-dependency of dispersal. Overall, our literature search did not yield many examples of variation in the effect of heterospecifics on dispersal with other abiotic and biotic context (but see some studies on the interplay between intraspecific and interspecific conditions [61–66], between habitat quality and predation risk [67,68], between abiotic conditions (*e.g.* sunshine, temperature) and diverse biotic conditions [69,70]). The interplay between biotic and abiotic environmental dimensions, phenotype, and dispersal can further make the relationship between interspecific interactions and dispersal complicated [59]. Dispersal is indeed a multi-causal process [71], responding to multiple internal and external cues that are themselves intertwined. For example, species

interactions strongly influence the density of interacting species. Predation, by decreasing prey density, would thereby decrease intraspecific competition [6] and potentially increase inbreeding. On the other hand, the response to intraspecific competition itself can vary with predation risk, as is the case in *Notonecta undulata* where the intraspecific density threshold for dispersal was shifted downwards when fish predator cues were present [61]. The effect of predation risk can further depend on the structure of the habitat, such as in hydropsychid larvae where the use of drift dispersal to avoid predators was favoured in structurally simple habitats, while habitats with a dense periphyton mat allowed sufficient microhabitat refugia from predators to decrease dispersal [67]. The resulting dispersal responses to this blend of central dispersal drivers are difficult to predict. Interestingly, studies manipulating only detrimental interaction cues led to a greater positive impact on the focal species' dispersal than the ones studying the actual presence of interacting species. Such stronger effects of cues can be related to the notion of landscape of fear [26,72], where the mere presence of predators can have stronger impacts than actual prey consumption. The type of cues affecting the dispersal response can vary depending on the species and their specific biology, such as on *Baetis thermicus* larvae where larvae detected the risk of predation by diurnal foragers such as salmon mainly through visual cues, increasing drift rate, while predation of the nocturnal sculpin was mainly detected through chemical cues [73].

The actual interaction strength between species, perceived within the actual study conditions, should therefore better predict the effect of the interactor's presence on dispersal [14]. However, only 43% of studies quantified the interaction strength along with dispersal responses, and thus we used indirect measures of interaction strength through the generalism of interacting partners towards each other (e.g. single or multiple predator species for a focal prey species). We found that the level of generalism of interacting species affected the dispersal outcome. Counterintuitively, the level of generalism of the focal species was mainly important for detrimental interactions, where positive effects of interactor presence on dispersal were strongest for more generalist focal species, while the level of generalism of the interacting species was more important for beneficial interactions, with a stronger negative impact for more generalist interactors. We were expecting the level of interactor generalism to be of stronger importance for detrimental interactors, as for example prey might have a higher motivation to escape highly

specialized predators than generalist predators. Further, we were expecting that more specialized focal species may pose a broader burden on their resource, increasing demographic fluctuations and thus extinction probability of the focal species, leading to a stronger effect on dispersal [17].

We further screened articles and the broader literature to gather information about interaction strength between pairs of species, resulting in variation in the populations or study condition used (densities and type of species manipulation) in the studies on dispersal and interaction strength, a potential source of discrepancies [60]. Further, the interaction strength was measured through fitness-related traits that varied among pairs of interacting species (*i.e.*, survival, fecundity, body condition and abundance). While this result should be taken with caution, although the approach should be conservative, the estimated strength of interactions between species predicted the dispersal responses to interaction well, and even better than using the binary beneficial/detrimental type of interaction (Table S7). When restricting our dataset to studies jointly measuring the dispersal response and interaction strength, we even better estimated the effect of interaction strength on dispersal. These results demonstrate the importance of assessing interaction strengths and fitness consequences concomitantly with dispersal dependencies, in single and multiple conditions, to better understand interaction-dependent dispersal and why it varies among species, interaction types, and ecosystems (Fig. 1).

Our results further showed that the effects of interactors varied with the dispersal phase studied. Detrimental interactions had stronger positive impacts on emigration than on full dispersal, and even had negative impacts on transience. We expected predators, parasites, and competitors to increase the dispersal of the focal species to avoid the potential negative consequences on fitness, and this was the case for emigration and full dispersal [15,74]. However, transience is a particularly vulnerable stage where the risk of predation may be heightened; thus, a decrease in dispersal distance for instance may be expected. Similarly, hosts may increase their dispersal behaviour to escape an infested habitat [15], and parasites themselves can manipulate their hosts' dispersal to increase contact rate and the transmission of parasites [21]. However, by diverting their hosts' resources, parasites can constrain their ability to move [21]. Such contrasted effects of parasitism can be illustrated by a study on *Notonecta*, where parasite infection reduced *Notonecta* dispersal ability, but parasitism risk



increased dispersal distance [75]. We thus expected factors influencing emigration decisions and dispersal distance to be fundamentally different, with emigration decisions varying solely with local conditions and dispersal distance varying with the ability to disperse and the spatial scale of the interaction. The impact of beneficial interactions also depended on the dispersal phase studied, with strong negative impacts on emigration, slightly weaker impacts on transience and no effect on full dispersal. The difference between effects of beneficial and detrimental interactors might reflect a dependency on both the local and the broader spatial context for detrimental interactors, while the local context was the main driver of dispersal decisions for beneficial interactors. Again, a more precise estimate of the scale and decay of interaction strength through the landscape and its effects on focal species fitness at each dispersal phase may help resolve this question. The information we could gather on species home range was fairly limited, but we found that the ratio of home ranges influenced the focal species dispersal, with a tendency for larger home ranges for focal species relative to the interactor decreasing the dependency of dispersal on detrimental interactions. This larger home range may allow focal species to escape detrimental interactors through changes in spatial distribution within their habitat, a likely less costly strategy than dispersing away. The interplay between species interaction and dispersal at different spatial scales should play an important role for metacommunity dynamics. Indeed, a recent theoretical study has shown that the spatial scales of dispersal and species interactions have opposite effects on ecosystem functioning [76]. A modelling effort illustrating the impacts of context-dependent dispersal in simple three-level food chain communities shows that simultaneous resource- and predator-dependent emigration reduced local fluctuations of population dynamics through time, and increased metacommunity stability [13]. In competitive communities of two *Callosobruchus* species, subdivision of the habitat into patches within a metacommunity structure allows for new niche differentiating mechanism through a dispersal-competition trade off allowing species coexistence [77]. Further, the dependency of dispersal on spatial scale should itself depend on the spatiotemporal autocorrelation of population dynamics between interacting species across scales [6,13,18], potentially leading to the co-evolution of dispersal of interacting species [17].

We were also expecting the impact of the interacting species to depend on the larger biotic context.

Specifically, we expected that more complex communities could lead to a “dilution effect” where the cues and the impact of each interacting species on the focal species’ dispersal may be weaker when diluted in a larger number of species interactions. We observed the opposite effect, with stronger positive effects of detrimental interactors being observed in more complex communities than for studies on pairs of interacting species. This could be explained by methodological differences between studies on pairs of interacting species, very often laboratory studies, and studies on more complex communities, often corresponding to field studies or semi-natural mesocosm studies. Oversimplified set-ups may actually buffer the effects of interaction on dispersal through acclimation to threats and an overall lower perception of risk. Because of the inherent nestedness of community complexity and experimental set-up, we were not able to put both moderators in the models. An alternative explanation rests on a confounded effect of multiple species interactions. As mentioned above, field studies often lead to difficulties in disentangling effects on survival from effects on dispersal and in properly isolating the effect of a single species. For example, the abundances of a prey species and its different predator species are often correlated, leading to difficulties in isolating the effect of each predator species without intensive monitoring of all species at play [78]. The same reasoning can be made for other interacting species like resources for consumers, as in flying squirrels which depend on multiple resources (spruce, birch and alder catkin), that likely covary and can alternatively appear as the main driver of fitness [79,80], potentially hampering the estimate of their respective effects on dispersal.

Finally, we showed that the duration of the study modulates the effects of interactions on the dispersal of focal species. The longer the study lasted the closer the effect sizes were to zero for detrimental interactions, and to a lower extent for beneficial interactions. This effect may reflect an acclimation to the interacting species in experimental studies, reducing the sensitivity of individuals to stressful interactions and therefore their dispersal propensity to avoid them. In addition, not all individuals are equally likely to disperse [4] and/or to respond through dispersal to adverse abiotic and biotic conditions [55,81]. Shorter experiments may capture the most responsive individuals and the longer the study lasts the weaker the overall response should be. However, one can alternatively argue that less responsive individuals would also react and disperse only after long-lasting experiments. Unfortunately, dispersal studies are often limited in time or space and might

therefore misestimate the effect of interaction-dependent dispersal at the whole population scale.

Our systematic literature review focused only on actively dispersing species, and thus excluded passively dispersed taxa such as plants. It yielded a majority of articles on insects, with other groups like spiders, birds, nematodes, mammals, or protists being less represented. While our dataset was taxonomically biased, it matched the taxonomic coverage of the systematic review on intraspecific density [19], and showed much lesser taxonomic bias than behavioural studies for instance [50]. This highlights the importance of covering a wide range of taxa across the phylogenetic tree in dispersal studies to account for the diversity of dispersal behaviours and species interactions. Another knowledge gap highlighted by our literature search is the relative lack of studies on the interplay between species interaction and dispersal syndromes (but see [82–86] in our database). Given the suggested role of dispersal syndromes in fitness-dispersal relationship and eco-evolutionary dynamics of metacommunities [55,81], we would suggest that research groups integrate a more detailed characterisation of the phenotype and its relationship to dispersal into their studies. Further, a meta-analysis focusing on passively dispersing species would help to understand whether processes influencing interaction-dependent dispersal are similar to those affecting active dispersers. Finally, we want to highlight the following conclusions and ideas to stimulate further research on dispersal and species interaction:

#### (1) Methodological issues :

- (a) The **experimental set-up** matters. Oversimplified set-ups may buffer effects of interactions on dispersal through acclimation to threats. On the other hand, field studies often prevent disentangling effects of biotic conditions on survival and dispersal. Further, they can struggle to isolate properly the effect of each species interaction on the dispersal of a focal species because interactions among different interacting species (*e.g.*, interaction of a prey species with multiple predator species) often covary in time or space. Those issues are at the core of discussions on **experimental vs. observational approaches**. Large-scale experiments in more realistic ecological conditions monitored over time as well as a more holistic investigation of biotic and abiotic drivers in the field might improve our understanding of the relationship between dispersal and species interactions.

- (b) **The duration of the experiment** largely influences the estimated relationship between dispersal and species interaction. It does not mean we should run shorter experiments to increase the likelihood of finding larger effects because species interactions and dispersal phases last longer in nature than in an experiment. However, we should consider the temporal aspect as an additional factor when running an experiment manipulating species interactions on varying time windows and select appropriate durations relative to species' generation time. In addition, natural contexts often imply the **integration of cues** on interacting species **over a larger temporal window** within and between generations, thereby providing a more realistic estimate of information acquisition in stable and predictable environments and a poor estimate of enduring species interaction in changing environments.

- (c) **Cues** might lead to stronger effects than the **actual presence** of an interacting species. A potential reason to consider is that the actual presence often mixes direct effects of the interaction, including numerical effects of it (*i.e.*, predators consume prey), and species behavioural responses. For example, prey may intend to respond to cues about predation risk by leaving its habitat, but this intent might be repressed by the immediate lethal costs of doing so when actual predators are present. Such impacts of cues can be related to the landscape of fear, whereby predators have a disproportionately strong effect on prey redistribution over the landscape compared to their direct consumptive effect [26,72]. This landscape of fear effect also implies that measuring interaction strength by fitness effects alone might underestimate its ecological impact mediated by behaviour.

#### (2) Ecological aspects of interaction-dependent dispersal

- (d) The numerical effects of species interactions further influence **intraspecific competition** through changes in population density. This main driver likely influences species fitness and dispersal propensity in an opposite direction to species interactions. Beneficial interactions likely increase population density while detrimental interactions decrease it [6]. The resulting consequence for dispersal calls for study designs testing the respective and

interactive effects in a fully crossed manner [59].

- (e) A clear pattern is the effects of **dispersal phase**. It has been pointed out repeatedly [4,5] that aside from our naïve expectation that emigration and immigration decisions should mirror each other, the risk and benefits of species interaction likely vary between initial habitat, environments crossed during transience and new habitats to settle in. It appears important to investigate the fitness and dispersal consequences of species interactions through the three movement phases. A further review should focus on the consequences of interspecific interactions at the colonisation stage.
- (f) We need to improve our understanding of the **spatiotemporal dynamics** of interacting species. Indeed, dispersing from its current or natal habitat is a behavioural decision with large and lasting consequences for individual life history [87]. Therefore, alternative responses to a threat might be favoured when the population dynamics of interacting species give room to those alternatives (*e.g.*, asynchrony in predator and prey population dynamics). Modelling studies have shown the importance of spatiotemporal autocorrelation for dispersal dynamics [6,13,18]
- (g) The dispersal response depends on the **interaction strength**. We have shown that beneficial and detrimental interactions lead to opposite dispersal responses, but the effect can be modulated by the type of interaction, the level of specialization between interactors, and the dilution of the interaction by community diversity. More studies should aim at characterising this interaction strength, from the local community level to higher spatial scales in a metacommunity context, to better understand its impacts on dispersal.
- (3) **Ecological and evolutionary consequences for metacommunities**
- (h) **Moving from pairs of species to complex metacommunities** may be a difficult task. We have shown that the importance of context-dependent dispersal depends on the overall community context, thus experiments with pairwise interactions may fail to capture the complexity of the dispersal response and studies in natural communities may fail to tease apart the respective and interactive

effects of multiple interactions. Nevertheless, modelling studies show that with even simple three-level communities, context-dependent dispersal between pairs of species has a strong impact on metacommunity dynamics [13].

- (i) **Context-dependent dispersal should shape metacommunity dynamics**. When studying the consequences of dispersal at the landscape level, studies often treat dispersal as a constitutive trait of species and/or landscape features [76]. Our results evidence a dispersal plasticity in response to biotic interactions, particularly in the context of the landscape of fear [26,72], which should influence the species distribution and their match to local ecological conditions within a landscape.
- (j) We need to better understand how **evolving landscapes can affect the context-dependency of dispersal**. Eco-evolutionary dynamics of species interactions should influence the evolution of both context-independent [17] and context-dependent dispersal [6,55], and conversely the eco-evolutionary dynamics of dispersal should influence species interactions and metacommunity dynamics [55]. These two evidenced assertions hamper the accurate predictions of metacommunity dynamics in a greatly and rapidly changing world.

**Data and materials availability:** Data and code are available on Zenodo (<http://dx.doi.org/10.5281/zenodo.10940162>).

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## SUPPLEMENTARY MATERIAL

### Box S1: Full description of the keywords for the meta-analysis.

The search was conducted on Web of Science on the 20th of October 2021 and yielded 21499 results.

*TS=(predat\* OR resource\* OR prey\* OR parasit\* OR host\* OR compet\* OR facilitat\* OR mutualis\* OR cooperat\* OR phore\* OR commensal\* OR interspeci\* OR heterospeci\* OR context\* OR condition\* OR metacommunit\* OR "mutual inhibition" OR ammensalis\* OR symbio\*)*

*AND TI=(dispers\* OR migrat\* OR emigrat\* OR immigrat\* OR colonis\* OR coloniz\* OR nomadi\*)*

*NOT TI=("seasonal migration" NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=("vertical migration" NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=("autumn migration" NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=("fall migration" NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=("spring migration" NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=(catadrom\* NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=(anadrom\* NOT dispers\* NOT emigrat\* NOT immigrat\* NOT colonis\* NOT coloniz\*)*

*NOT TI=(dispersion OR dispersible)*

*NOT TS=(refugees OR "international migration" OR "domestic migration" OR "human migration" OR asylum OR illegal)*

*AND (SJ=("ENVIRONMENTAL SCIENCES ECOLOGY" OR "ZOOLOGY" OR "BEHAVIORAL SCIENCES" OR "BIODIVERSITY CONSERVATION" OR "INFECTIOUS DISEASES" OR "PLANT SCIENCES" OR "PHYSIOLOGY" OR "LIFE SCIENCES BIOMEDICINE OTHER TOPICS" OR "AGRICULTURE" OR "MARINE FRESHWATER BIOLOGY" OR "MICROBIOLOGY" OR "PATHOLOGY" OR "EVOLUTIONARY BIOLOGY" OR "DEMOGRAPHY" OR "ENTOMOLOGY" OR "PARASITOLOGY" OR "FORESTRY" OR "FISHERIES"))*

*NOT (WC=("PUBLIC ENVIRONMENTAL OCCUPATIONAL HEALTH" OR "ETHNIC STUDIES" OR "ECONOMICS" OR "PHARMACOLOGY PHARMACY" OR "FOOD SCIENCE TECHNOLOGY" OR "REGIONAL URBAN PLANNING" OR "CHEMISTRY ANALYTICAL" OR "GREEN SUSTAINABLE SCIENCE TECHNOLOGY" OR "ANTHROPOLOGY" OR "GASTROENTEROLOGY HEPATOLOGY" OR LAW OR "PSYCHOLOGY BIOLOGICAL" OR "ENERGY FUELS" OR "MEDICINE RESEARCH EXPERIMENTAL" OR ONCOLOGY OR "DENTISTRY ORAL SURGERY MEDICINE" OR "RADIOLOGY NUCLEAR MEDICINE MEDICAL IMAGING" OR "NUTRITION DIETETICS" OR "CHEMISTRY PHYSICAL" OR "RESPIRATORY SYSTEM" OR PALEONTOLOGY OR SOCIOLOGY OR "PERIPHERAL VASCULAR DISEASE" OR "PEDIATRICS" OR "SOCIAL SCIENCES BIOMEDICAL" OR "ASTRONOMY ASTROPHYSICS" OR "BIOPHYSICS"))*



## Box S2: Full model equations for both the full dataset and the beneficial/detrimental interactor dataset

The models were run with the *metafor* v 4.2-0 package [47] in R v4.3.1. We used the dredge function from the *MuMIn* v 1.47.5 package to select models with the best fixed structure from the full models, and averaged models within  $\Delta AIC_c < 2$ .

### # full model for the full dataset

```
full_mod_all = rma.mv(yi=es, v=var,

mods=~ type_interactor * dispersal_phase + type_interactor * type_study + type_interactor *
type_manipulation_interactor + type_interactor * type_community + type_interactor * possibility_interactor_disperse +
type_interactor * generation_similarity +
  type_interactor * I(level_generalism_focal - mean(level_generalism_focal)) + type_interactor *
I(level_generalism_interactor - mean(level_generalism_interactor)) + type_interactor * I(log_generation_time_focal -
mean(log_generation_time_focal)) + type_interactor * I(log_duration_experiment - mean(log_duration_experiment)),

random= list(~1 | study_ID, ~1 | focal_ID, ~1 | interactor_ID), R = list(focal_phylo=focal_phylogenetic_tree),

method='ML', test='t', data= full_dataset)
```

### # full model for beneficial interactors

```
full_mod_beneficial = rma.mv(yi=es, v=var,

mods=~ nature_interactor + dispersal_phase + type_study + type_manipulation_interactor + type_community +
possibility_interactor_disperse + generation_similarity +
  I(level_generalism_focal - mean(level_generalism_focal)) + I(level_generalism_interactor -
mean(level_generalism_interactor)) + I(log_generation_time_focal - mean(log_generation_time_focal)) +
I(log_duration_experiment - mean(log_duration_experiment)),

random= list(~1 | study_ID, ~1 | focal_ID, ~1 | interactor_ID), R = list(focal_phylo=focal_phylogenetic_tree),

method='ML', test='t', data= beneficial_interactors_dataset)
```

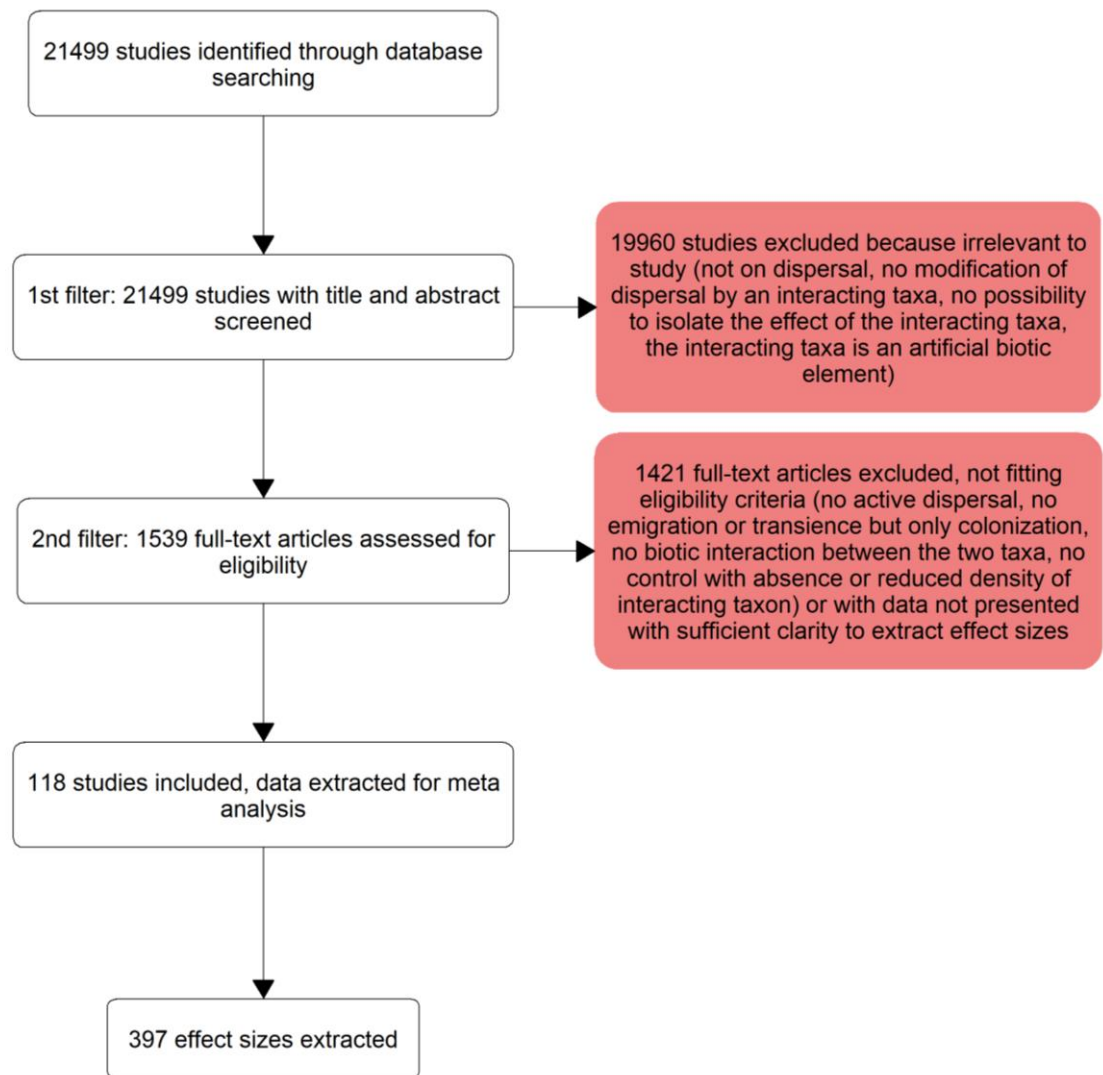
### # full model for detrimental interactors

```
full_mod_detrimental = rma.mv(yi=es, v=var,

mods=~ nature_interactor + dispersal_phase + type_study + type_manipulation_interactor + type_community +
possibility_interactor_disperse + generation_similarity +
  I(level_generalism_focal - mean(level_generalism_focal)) + I(level_generalism_interactor -
mean(level_generalism_interactor)) + I(log_generation_time_focal - mean(log_generation_time_focal)) +
I(log_duration_experiment - mean(log_duration_experiment)),

random= list(~1 | study_ID, ~1 | focal_ID, ~1 | interactor_ID), R = list(focal_phylo=focal_phylogenetic_tree),

method='ML', test='t', data= detrimental_interactors_dataset)
```



**Figure S1: Prisma plot**

Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA, [30]) diagram showing how records were assessed, screened, and included in the meta-analysis.

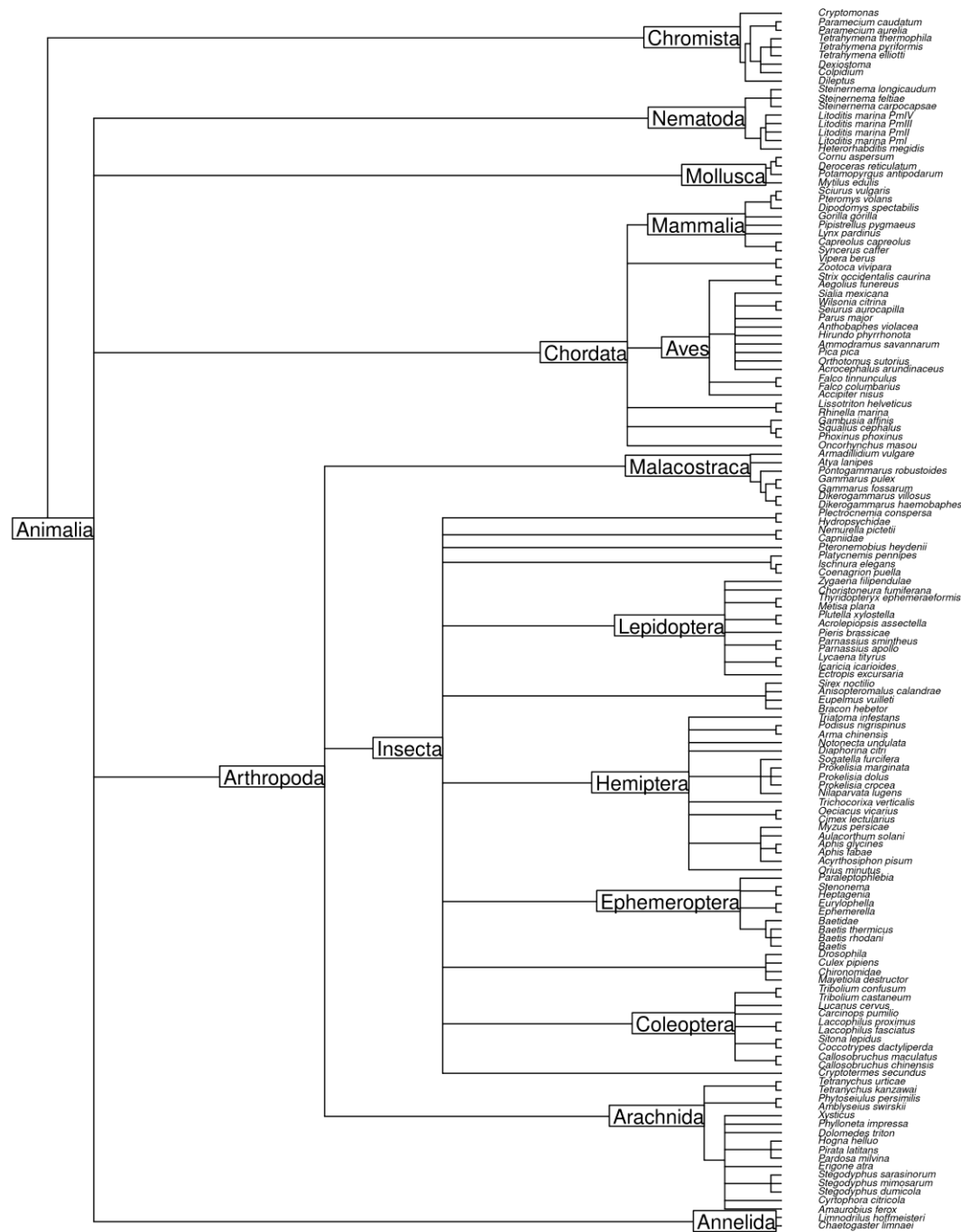
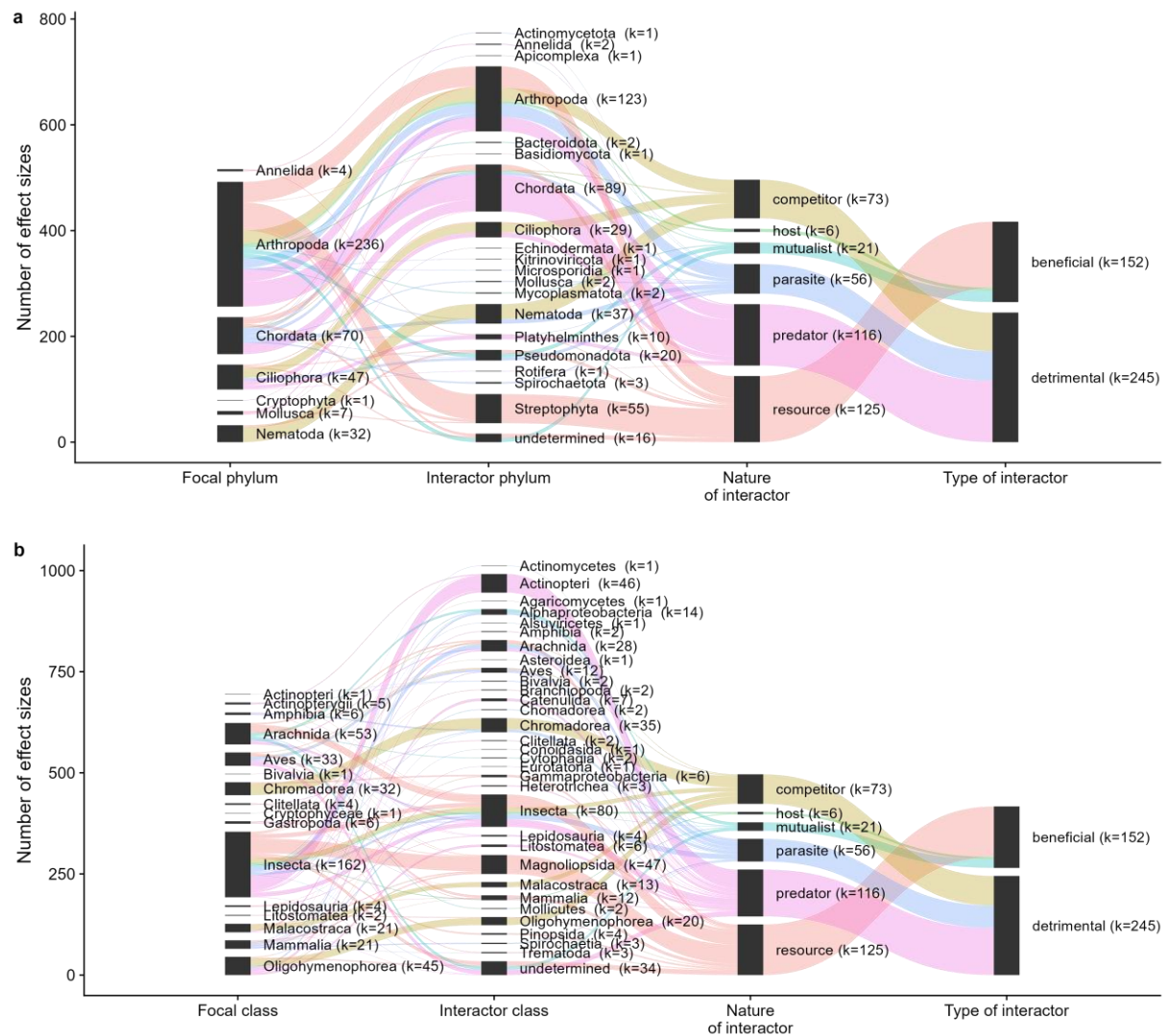


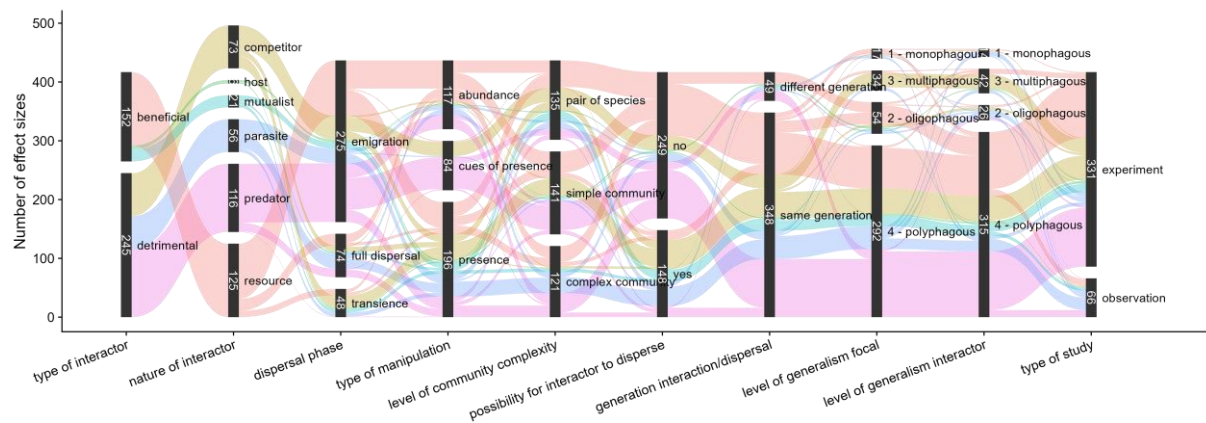
Figure S2: Phylogeny of the focal taxon

The taxonomy of the focal taxa extracted from the GBIF database (and other databases when missing) is used as a surrogate for a true phylogenetic tree, with Graphen’s method for compiling branch length [46].



**Figure S3: Taxonomic description of the taxa involved in the analysis**

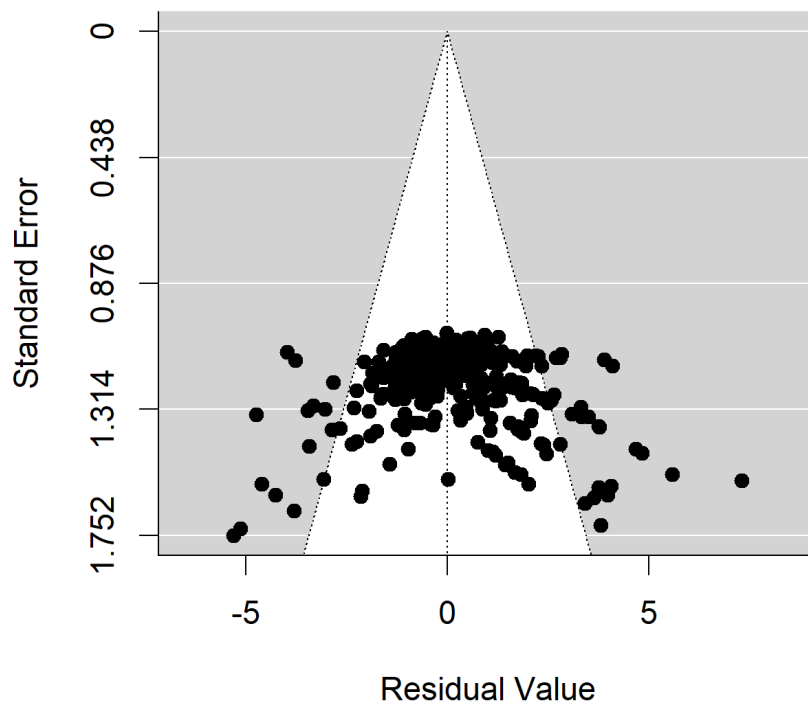
(a) Sankey diagram of the number of effect sizes (k) per focal taxon phylum, interacting taxon phylum, type of interactor (beneficial/detrimental) and nature of interactor, coloured by the nature of interactor (red: resource, pink: predator, dark blue: parasite, teal blue: mutualist, forest green: host, yellow-green: competitor). (b) Sankey diagram this time per focal class and interacting taxon class.



**Figure S4: Number of effect sizes by moderator level for the main moderators**

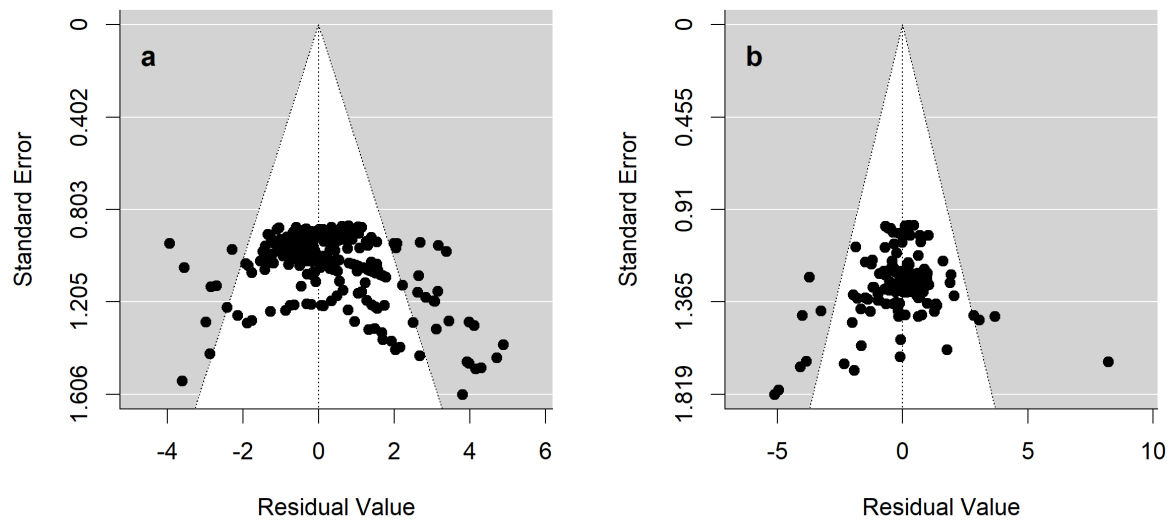
Sankey diagrams of the number of effect sizes ( $k$ , in white inside the bars) per moderator for all of the moderators of interest, i.e. the type of interactor (detrimental or beneficial interactor), the nature of interactor (competitor, host, mutualist, parasite, predator, resource), the dispersal phase (emigration, full dispersal or transience), the type of manipulation of the interactor (presence, cues of presence, abundance), the level of community complexity (pair of species, simplified community or complex community), the possibility for the interactor to disperse, the similarity in generations between the interaction and the dispersal (same or different generation), the level of generalism of the focal species and of the interactor (rated from 1 to 4), and last the type of study (experimental or observational). Colours corresponds to the nature of interactor (red: resource, pink: predator, dark blue: parasite, teal blue: mutualist, forest green: host, yellow-green: competitor).





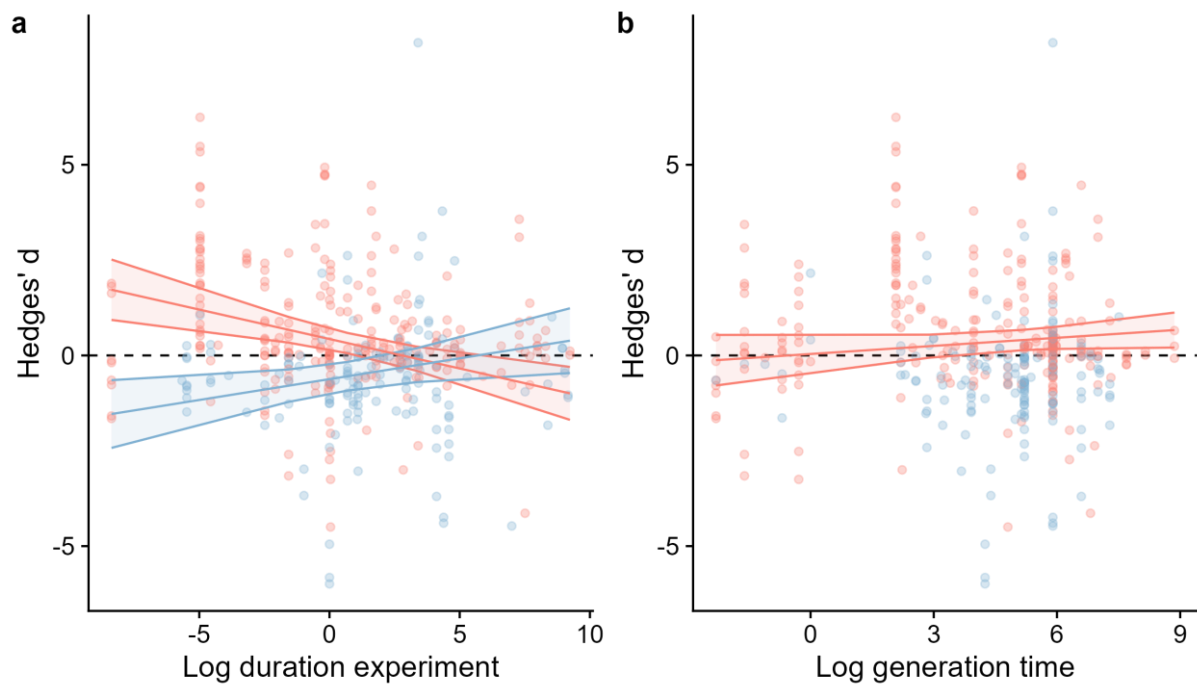
**Figure S5: Funnel plot of the model with all moderators represented in the averaged model**

The funnel plot on the model containing all moderators represented in the averaged model does not evidence any strong asymmetry, which is confirmed by the Egger's test that shows that the intercept for the residuals by precision linear model crosses zero (intercept [95% CI] = 0.13 [-0.03, 0.28],  $t = 1.6$ ,  $df = 395$ ,  $p = 0.119$ ). Together with the very high Rosenberg fail-safe number ( $N = 47929$ ), this suggests that there is no evidence of publication bias.



**Figure S6: Funnel plots of the models for the two data subsets with all moderators represented in the averaged models**

(a) Funnel plot for detrimental interactions, (b) Funnel plot for beneficial interactions. The funnel plot for detrimental interactions reveals some asymmetry, which is confirmed by the Egger's test that shows a non-zero intercept for the residual (intercept [95% CI] = 0.30 [0.11, 0.48],  $t = 3.2$ ,  $df = 243$ ,  $p = 0.002$ ), suggesting potential publication bias. However, the Rosenberg fail-safe number was very high ( $N = 30,695$ ), suggesting the converse. For beneficial interactions, the Funnel plot does not evidence any strong asymmetry, which is confirmed by the Egger's test (intercept [95% CI] = -0.21 [-0.64, 0.22],  $t = -0.98$ ,  $df = 150$ ,  $p = 0.33$ ). Together with the high Rosenberg fail-safe number ( $N = 17,746$ ), this suggests that there is no evidence of publication bias.



**Figure S7: The effect of interactors on dispersal varies with the duration of the experiment and the generation time**

Effect of (a) the log duration experiment or (b) the log generation time and type of interactor (red: detrimental, blue: beneficial) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Points represent the effect sizes, and lines and confidence intervals are displayed from marginal means and 95 % CI from the two meta-analytic models calculated at the minimum, Q1, median, mean, and maximum values of log duration.

**Table S1: Effect size transformation depending on the type of data.**

The preferred type of data extracted was either pair of means, contingency tables or correlation (depending on the type of study), followed by test parameters from t-tests, F-tests or other types of tests.

Type of data	Data extraction	Reference and R functions used	Formula
Pair of means	From raw data, from tables or text, from figures with means and SE, means and SD, or boxplots [18]	[37] esc ::esc_mean_sd	$d = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1+n_2-2}}} J,$ <p>where <math>J = 1 - \frac{3}{4(n_1+n_2-2)-1}</math>  and <math>v_d = \frac{n_1+n_2}{n_1n_2} + \frac{d^2}{2(n_1+n_2)}</math></p>
Contingency table or log odds ratio	From raw data, tables or text, occasionally from figures. Either number of dispersers (A: treatment, B: control) and residents (C: treatment, D: control) per category, or log odds ratio and variance extracted from summary data from logistic models and logistic mixed models	[34,37] esc ::esc_2x2	$\frac{AD}{BC'}$ <p>With <math>v_{lnOR} = \frac{1}{A} + \frac{1}{B} + \frac{1}{C} + \frac{1}{D}</math>,  Converted to Hedges' d following:</p> $d = \frac{\ln(\frac{AD}{BC'})\sqrt{3}}{\pi}$ <p>And</p> $v_d = \frac{3v_{lnOR}}{\pi^2}$
Correlation	From raw data, figures, tables or text	[34]	<p>Conversion to Hedge's d following</p> $d = \frac{2r}{\sqrt{1-r^2}}$ <p>And <math>v_d = \frac{4v_r}{(1-r^2)^3}</math></p>
Student t test, F-test from one-way ANOVA	From tables or text	[37,38] esc ::esc_t	$ r  = \sqrt{\frac{t^2}{t^2+df}} \text{ or }  r  = \sqrt{\frac{F}{F+df}}$

			Followed by a conversion from r to Hedge's d (see above)
X <sup>2</sup> coefficient from 2x2 frequency tables	From tables or text	[37] esc ::esc_chisq	$ r  = \sqrt{\frac{X^2}{n}}$ <p>Followed by a conversion from r to Hedge's d (see above)</p>
Mann-Whitney Z-score, Wilcoxon signed-rank test for paired samples	From tables or text	[38] effectsize ::z_to_d	$r = \frac{Z}{\sqrt{n}}$ <p>Followed by a conversion from r to Hedge's d (see above)</p>
Partial eta <sup>2</sup> from multiple factor ANOVA, from multiple factor regression, from linear mixed models, eta <sup>2</sup> from Kruskal-Wallis H-test	From tables or text	[38–40] esc ::cohens_d	$\eta_p^2 = \frac{SS_{effect}}{SS_{effect} + SS_{error}}$ $\eta_p^2 = \frac{F * df_{effect}}{F * df_{effect} + F * df_{error}}$ $\eta_p^2 = \sqrt{\frac{t^2}{t^2 + df}}$ $\eta_h^2 = \frac{H - k + 1}{n - k}$



**Table S2: Types of moderators and simplification of information**

For each type of moderator/random effect, we describe the levels and the number of effect sizes (es) per level, as well explain the choices made to create the moderator.

Name of moderator/random effect	Levels	Choices on moderator
Study ID	118 levels, the ID of the study	
Focal taxon identity, taxonomy and phylogeny	<p>Focal taxon identity: 144 levels, genus: 116 levels, family: 94 levels, order: 41 levels, class: 16 levels, phylum: 7 levels, kingdom : 2 levels.</p> <p>Correlation matrix between focal taxa from phylogeny.</p>	<p>Focal taxon identity gathered from the study, normally species ID but can be genus (17 effect sizes) or family (12 es) depending on the study.</p> <p>Focal taxon taxonomy gathered from the NCBI database with taxize R package v0.9.100; when missing from GBIF or ITIS databases.</p> <p>Focal taxon phylogeny created from surrogate taxonomic tree with grafens method to compute branch length.</p>
Interacting taxon identity, taxonomy	Interacting taxon identity: 165 levels, genus :125 levels, family: 103 levels, order: 69 levels, class: 32 levels, phylum: 20 levels, kingdom 7 levels.	Interacting taxon identity gathered from the study, normally species ID but the taxon can be determined at several taxonomic levels up to the kingdom or include undefined groups ( <i>e.g.</i> , dead wood, microalgae). We gathered interacting taxon taxonomy from the same databases as focal taxon, and to avoid missing data we replaced all NA by « undetermined ». Because of the number of undetermined data, as well as the number of groups defined to higher taxonomic levels, we did not provide a phylogeny.
Nature of interactor	6 levels, resource (125 es), competitor (73 es), host (6 es), mutualist (21 es), parasite (56 es), predator (116 es). Reference level: resource	We grouped parasites, parasitoid and virus as the « parasite » category, we grouped prey and resource as « resource », and endosymbiont and defensive mutualist as « mutualist ».
Type of interactor	2 levels, detrimental (245 es) or beneficial (152 es). Reference level: detrimental	We assumed that competitors, parasites and predators reduce the fitness of the focal species and are thus detrimental interactors, while resources, hosts and mutualists enhance the fitness and are thus beneficial

		interactors.
Type of community	3 levels: pair of species (135 es), simple community (141 es) or complex community (121 es). Reference level: pair of species.	Studies either manipulated two taxa alone, manipulated a focal taxa and an interacting species in a simplified community composed of a small subset of species (often resources, but sometimes more complex), or manipulated the focal taxa and the interacting taxa in more complex settings including a large number of taxa ( <i>e.g.</i> , manipulative studies in the wild with addition of predator cues or resources). Further, studies that did not manipulate the interacting species presence or abundance could also be classified in these levels ( <i>e.g.</i> , observational studies correlating the abundance of predators and the dispersal of the focal taxon).
Type of manipulation	3 levels: presence (196 es), cues of presence (84 es), or abundance (117 es). Reference level: presence	Studies could either manipulate the presence or the cues of presence of the interacting species, in a 0/1 setting, or manipulate the abundance (or abundance of cues) in a gradient or by comparing levels. Because only one study manipulated the cues of abundance, with only 4 es, we merged the effect sizes of direct manipulation of abundance with the cues of abundance effect sizes to create only three levels, presence, cues of presence, or abundance. Observational studies could also be classified in these three levels.
Possibility for the interactor to disperse	2 levels: no (249 es) or yes (148 es). Reference level: no	The question here is can the interacting taxon disperse during the experiment/observation, and not can it disperse overall.
Dispersal phase	3 levels: emigration (275 es), transience (48 es) and full dispersal (74 es). Reference level: emigration	Dispersal phase studied during the experiment/observation, either emigration, transience or full dispersal where individuals were monitored from the emigration to the immigration phase. Studies focusing only on the colonization part were excluded.
Similarity of generation between interaction and dispersal	2 levels: same generation (348 es) or different generation (49 es). Reference level: same generation.	Is the dispersing individual the same as the interacting individual? In most of the cases, the dispersing individual is the individual that has undergone the interaction, but in certain cases, it can be its parent ( <i>e.g.</i> risk of predation on the parent and observed dispersal of the offspring) or its offspring ( <i>e.g.</i> nest predation where the parent disperses after a predation

		on its offspring)
Type of study	2 levels: experiment (331 es), observation (66 es). Reference level : experiment	Either experimental studies, or observational studies in the field.
Experimental setting	3 levels: laboratory (213 es), semi-natural (74 es) or <i>in natura</i> (110 es). Reference level: laboratory	Laboratory studies regroup studies in indoors microcosms or mesocosms, dispersal arenas or wind tunnels, while semi natural studies are outdoors mesocosms or some greenhouse and volary studies, and the last category are field studies. Note that because this moderator was nested within the type of community moderator, and thus difficult to disentangle, and because we were more interested in biological questions that methodological ones, we excluded this moderator.
Duration of the experiment	Numerical, centered log number of days.	Duration of the experiment or observation. The number of days varies between $-2e-4$ days and $1e5$ days, with a Q1 of 0.2 days, a median of 2 days, a Q3 of 28 days. We use the log number of days.
Generation time of the focal species	Numerical, centered log number of days	This moderator was either extracted from the studies when available, or more often found in a second step of searching the larger literature. The number of days varies between 0.1 and 7044, with a Q1 of 18, a median of 170 and a Q3 of 365. We use the log number of days.
Level of generalism of the focal species + Level of generalism of the interactor	Numerical, range 1-4.	This moderator was found in a second step of searching the larger literature. We rated focal and interacting species from 1 to 4 on whether they eat only one species, from the same genus or family, from the same order, or from different orders. Most of the species fell into the polyphagous category (rated 4: 292 es for focal species and 315 for interactors), with other ranging from 34 es for focal and 42 for interactors rated 3, 54 es for focal and 26 for interactors rated 2, and 17 es for focal and 14 for interactors rated 1 (monophagous).
Home range of the focal species + Home range of the interactor	Numerical	This moderator was found in a second step of searching the larger literature. Unfortunately, this information was available for very few pair of species, thus it is not included in the main models but tested for separately

		on a small subset of 17 effect sizes. We use the log ratio of home range focal/home range interactor.
Interaction strength between species	Numerical	This moderator measures the interaction strengths between pairs of species found in the database as a standardize effect of the presence or abundance of the interacting species on a fitness-related traits in focal species (survival, fecundity, body condition, body growth, or abundance). The information was found either in the primary literature (studies that measured both dispersal and interaction strength, 166 es) or on the secondary literature (studies on interactions between pairs of species, 191 es). We were not able to find interaction strength data for 40 es in our database. Because we used different response metrics with very different ranges ( <i>e.g.</i> , survival on a 0-1 scale vs fecundity 10000 eggs), we first centered the dependent variable by dividing by the mean variable value allowing to estimate proportional changes while maintaining metrics' variation. Then, we regressed the response metric depending on the occurrence (0 vs. 1) or the density of the interacting species mean-centered and scaled by standard deviation. The interaction strength ranges between -1.64 and 1.42, with a Q1 of -0.29, a median of -0.08 and a Q3 of 0.14.

**Table S3: Evaluation of the taxonomic bias of the dataset**

Comparison of the number of effect sizes per taxonomic level in our database to the actual number of described species in each taxon taken from the Catalogue of Life version 2023-11-24 (<https://www.catalogueoflife.org/>, [51]). Following [50], we used chi-square analyses to compare the observed numbers of effect sizes extracted from the publications in our database on taxa at two levels, kingdom and phylum, to expected frequencies generated from the recorded number of species in each taxon, under the null hypothesis that the representation of taxa in our database is in direct proportion to the relative number of species in that taxon.

Taxonomic level	Taxon	Nb of effect sizes	Nb of species	Expected frequency	Observed frequency	$\chi^2$
Kingdom						$\chi^2 = 68$ , df = 1, p = 2e-16
	Animalia	349	1,505,821	96 %	87.9 %	
	Chromista	48	62,581	4 %	12.1 %	
Phylum (among Animalia)						$\chi^2 = 354$ , df = 4, p = 2e-75
	Annelida	4	17,656	1.2 %	1.1 %	
	Arthropoda	236	1,171,751	82.9 %	67.6 %	
	Chordata	70	73,509	5.2 %	20.1 %	
	Mollusca	7	132,305	9.4 %	2 %	
	Nematoda	32	17,590	1.2 %	9.2 %	



**Table S4: Evaluation of time-lag bias for the meta-analytic model**

Model investigating the effect of time-lag bias by adding the interaction between the type of interactor (beneficial or detrimental) and the centered publication year to the model with all moderators retained in the averaged model. The effect sizes means, SE, 95 % CI, z-values and p-values are presented.

Moderator	Level	effect size	SE	95% CI	z-value	p-value
Intercept	intrcpt	-0.31	0.19	[-0.69,0.07]	-1.62	0.105
Dispersal phase	full dispersal	0.05	0.22	[-0.39,0.48]	0.21	0.837
	<b>transience</b>	<b>-1.38</b>	<b>0.35</b>	<b>[-2.06,-0.70]</b>	<b>-3.99</b>	<b>&lt;0.001***</b>
Centered log duration		<b>-0.15</b>	<b>0.04</b>	<b>[-0.22,-0.07]</b>	<b>-3.77</b>	<b>&lt;0.001***</b>
Centered level of generalism focal species		0.24	0.14	[-0.04,0.51]	1.69	0.092.
Type of community	<b>simple community</b>	<b>0.69</b>	<b>0.21</b>	<b>[0.28,1.11]</b>	<b>3.25</b>	<b>0.001**</b>
	<b>complex community</b>	<b>0.69</b>	<b>0.28</b>	<b>[0.14,1.25]</b>	<b>2.45</b>	<b>0.014*</b>
Type of interactor	beneficial	-0.34	0.19	[-0.70,0.03]	-1.81	0.070.
Type of study	observational	0.24	0.30	[-0.35,0.83]	0.78	0.433
Centered level of generalism interactor		<b>-0.23</b>	<b>0.10</b>	<b>[-0.43,-0.03]</b>	<b>-2.21</b>	<b>0.027*</b>
Type of manipulation of interactor	abundance	-0.15	0.11	[-0.36,0.06]	-1.38	0.168
	<b>cues of presence</b>	<b>0.44</b>	<b>0.19</b>	<b>[0.06,0.82]</b>	<b>2.29</b>	<b>0.022*</b>
Centered log generation time		0.05	0.04	[-0.03,0.13]	1.18	0.238
Similarity generation dispersal-interaction	different generation	0.27	0.28	[-0.28,0.82]	0.95	0.341
Type of interactor:Dispersal phase	beneficial:full dispersal	0.66	0.35	[-0.03,1.35]	1.88	0.060.
	<b>beneficial:transience</b>	<b>1.49</b>	<b>0.41</b>	<b>[0.67,2.30]</b>	<b>3.59</b>	<b>&lt;0.001***</b>
Type of interactor:Centered log duration	<b>beneficial:duration</b>	<b>0.25</b>	<b>0.06</b>	<b>[0.14,0.37]</b>	<b>4.31</b>	<b>&lt;0.001***</b>
Type of interactor:Type of study	<b>beneficial:observation</b>	<b>-1.48</b>	<b>0.50</b>	<b>[-2.47,-0.49]</b>	<b>-2.94</b>	<b>0.003**</b>
Type of interactor:Centered log generation time	beneficial:generation time	-0.08	0.06	[-0.19,0.03]	-1.45	0.146
Type of interactor:Centered level of generalism focal species	beneficial:generalism focal	-0.10	0.18	[-0.45,0.24]	-0.59	0.557
Type of interactor:Centered publication year	detrimental:year	0.00	0.01	[-0.03,0.03]	-0.19	0.848
	<b>beneficial:year</b>	<b>0.06</b>	<b>0.02</b>	<b>[0.03,0.09]</b>	<b>3.64</b>	<b>&lt;0.001***</b>

**Table S5: Meta-analytic means and 95 % CI by moderator for each of the two subsets of data**

Marginal means on the two meta-analytic models for beneficial and detrimental interactions, either averaged across all moderators or separated by type of moderator retained in the averaged model. The effect sizes means, SE and 95 % CI are calculated by the emmeans function from the emmeans package v1.8.8 on the models with all moderators maintained in the averaged model. Note for numeric variables, we present either results for the min, median and max values, or in the case of generalism, the min and max values (specialist and generalist).

Data subset	Moderator	Moderator level	Effect size	SE	95% CI
<b>Detrimental</b>	<b>Marginal means across all Moderators</b>		<b>0.328</b>	<b>0.136</b>	<b>[0.063,0.594]</b>
	Dispersal phase	<b>emigration</b>	<b>0.500</b>	<b>0.147</b>	<b>[0.211,0.789]</b>
		<b>full dispersal</b>	<b>0.513</b>	<b>0.227</b>	<b>[0.069,0.958]</b>
		<b>transience</b>	<b>-0.972</b>	<b>0.323</b>	<b>[-1.605,-0.339]</b>
	Log duration	<b>Min</b>	<b>1.723</b>	<b>0.404</b>	<b>[0.932,2.514]</b>
		<b>Med</b>	<b>0.324</b>	<b>0.135</b>	<b>[0.058,0.589]</b>
		<b>Max</b>	<b>-0.995</b>	<b>0.354</b>	<b>[-1.688,-0.301]</b>
	Type of manipulation	presence	0.102	0.166	[-0.224,0.427]
		abundance	-0.057	0.177	[-0.404,0.29]
		<b>cues of presence</b>	<b>0.866</b>	<b>0.211</b>	<b>[0.453,1.279]</b>
	Level of community complexity	pair of species	0.007	0.211	[-0.407,0.42]
		<b>simple community</b>	<b>0.434</b>	<b>0.201</b>	<b>[0.040,0.829]</b>
		<b>complex community</b>	<b>0.488</b>	<b>0.243</b>	<b>[0.013,0.963]</b>
	Level of generalism focal	mono	-0.358	0.271	[-0.890,0.173]
		<b>poly</b>	<b>1.015</b>	<b>0.273</b>	<b>[0.480,1.549]</b>
	Level of generalism interactor	<b>mono</b>	<b>0.601</b>	<b>0.214</b>	<b>[0.182,1.020]</b>
		poly	0.055	0.230	[-0.396,0.507]
	Type of study	experiment	0.268	0.144	[-0.015,0.550]
		observation	0.583	0.301	[-0.007,1.174]
	Log generation time	Min	-0.125	0.338	[-0.787,0.538]
		<b>Med</b>	<b>0.402</b>	<b>0.136</b>	<b>[0.136,0.668]</b>
		<b>Max</b>	<b>0.665</b>	<b>0.234</b>	<b>[0.207,1.123]</b>
	Possibility for interactor to disperse	no	0.225	0.198	[-0.164,0.613]
		<b>yes</b>	<b>0.457</b>	<b>0.187</b>	<b>[0.092,0.823]</b>

Data subset	Moderator	Moderator level	Effect size	SE	95% CI
<b>Beneficial</b>	Similarity in generations between dispersal and interaction	same generation	0.245	0.145	[-0.039,0.530]
		<b>different generation</b>	<b>1.057</b>	<b>0.356</b>	<b>[0.359,1.755]</b>
	Nature of interactor	predator	-0.002	0.205	[-0.404,0.400]
		<b>competitor</b>	<b>0.765</b>	<b>0.289</b>	<b>[0.198,1.331]</b>
		parasite	0.444	0.248	[-0.043,0.931]
	<b>Marginal means across all Moderators</b>		<b>-0.549</b>	<b>0.192</b>	<b>[-0.924,-0.173]</b>
	Dispersal phase	<b>emigration</b>	<b>-0.640</b>	<b>0.196</b>	<b>[-1.023,-0.256]</b>
		full dispersal	-0.132	0.254	[-0.629,0.366]
		transience	-0.555	0.291	[-1.125,0.015]
	Nature of interactor	<b>resource</b>	<b>-0.720</b>	<b>0.194</b>	<b>[-1.100,-0.339]</b>
		host	1.128	0.637	[-0.120,2.375]
		mutualist	-0.011	0.759	[-1.499,1.476]
	Level of generalism interactor	mono	0.318	0.417	[-0.498,1.135]
		<b>poly</b>	<b>-1.416</b>	<b>0.455</b>	<b>[-2.308,-0.524]</b>
	Log duration	<b>Min</b>	<b>-1.536</b>	<b>0.453</b>	<b>[-2.424,-0.648]</b>
		<b>Med</b>	<b>-0.546</b>	<b>0.192</b>	<b>[-0.921,-0.170]</b>
		Max	0.387	0.433	[-0.461,1.236]
	Type of study	<b>experiment</b>	<b>-0.470</b>	<b>0.203</b>	<b>[-0.868,-0.073]</b>
		<b>observation</b>	<b>-1.100</b>	<b>0.415</b>	<b>[-1.913,-0.287]</b>
	Level of generalism focal	<b>mono</b>	<b>-0.813</b>	<b>0.280</b>	<b>[-1.361,-0.265]</b>
		poly	-0.285	0.292	[-0.858,0.288]

**Table S6: Effect of home range ratio on the context-dependency of dispersal**

Model investigating the effect of interacting species' home range. Because we were not able to gather information on home range for most of the species pair, this is a separate model on the 17 effect sizes for detrimental interactions for which we were able to get the information. The model included the centered log ratio of home ranges (home range of the focal species/ home range of the interactor), as well as the study ID, focal species ID and interactor ID. The model had a total heterogeneity  $I^2$  of 39.7 %. The Egger's test showed no significant asymmetry (intercept [95% CI] = -0.03 [-0.21, 0.28],  $t = -0.29$ ,  $df = 15$ ,  $p = 0.77$ ). The effect sizes means, SE, 95 % CI, z-values and p-values are presented.

Moderator	effect size	SE	95% CI	z-value	p-value
Intercept	0.16	0.06	[0.05,0.28]	2.72	0.006**
Centered log ratio of home ranges	-0.02	0.01	[-0.05,0.00]	-1.73	0.084.

**Table S7: Effect of interaction strength on the context-dependency of dispersal**

Model investigating the effect of interaction strength on the focal species' dispersal, and their comparison to models investigating only binary interaction types (beneficial/detrimental). The models were done on two subset of studies: first on all data for which we were able to gather interaction strength information, from either the primary or the secondary literature ("All interaction strengths" dataset, 357 effect sizes over 108 studies), and second the data for which interaction strength was gathered from the primary literature ("Strict interaction strengths" dataset, 166 effect sizes over 51 studies). We compared through AICc models including the continuous interaction strength as a fixed effect and all random effects (study ID, focal species ID and phylogeny, interacting species ID) to models with the same random effects but binary interaction type as fixed effects. The Egger's tests showed some asymmetry for the dataset on all interaction strengths ( $p = 0.029$  and  $0.027$  for the intercept of models on interaction strength and type), but not for the strict dataset ( $p = 0.94$  and  $0.85$ ). All models had a large heterogeneity ( $I^2 = 97.8, 97.5, 97.2$  and  $96.6$  respectively for the models on interaction strength and on interaction type on all interactions, and the models on interaction strength and interaction type on the strict interaction database). The effect sizes means, SE, 95 % CI, z-values and p-values, as well as  $\Delta AICc$  between models, are presented.

Type dataset	Type model	Moderator	effect size	SE	95% CI	z-value	p-value	$\Delta AICc$	N
All interaction strengths	Model interaction strength	Intercept	-0.08	0.11	[-0.29,0.13]	-0.72	0.469	0.0	357
		Interaction strength	-0.72	0.13	[-0.98,-0.47]	-5.56	<0.001***		
	Model interaction type	Intercept	0.21	0.12	[-0.03,0.45]	1.72	0.085	16.5	
		Interaction type	-0.61	0.16	[-0.92,-0.30]	-3.91	<0.001***		
Strict interaction strengths	Model interaction strength	Intercept	-0.13	0.16	[-0.45,0.19]	-0.81	0.422	0.0	166
		Interaction strength	-1.24	0.20	[-1.64,-0.84]	-6.12	<0.001***		
	Model interaction type	Intercept	0.10	0.17	[-0.24,0.44]	0.58	0.561	32.8	
		Interaction type	-0.43	0.24	[-0.90,0.03]	-1.83	0.069		

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